Masticatory musculature of Asian taeniolabidoid multituberculate mammals

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The backward chewing stroke in multituberculates (unique for mammals) resulted in a more anterior insertion of the masticatory muscles than in any other mammal group, including rodents. Multituberculates differ from tritylodontids in details of the masticatory musculature, but share with them the backward masticatory power stroke and retractory horizontal components of the resultant force of all the masticatory muscles (protractory in Theria). The Taeniolabididae differ from the Eucosmodontidae in having a more powerful masticatory musculature, expressed by the higher zygomatic arch with relatively larger anterior and middle zygomatic ridges and higher coronoid process. It is speculated that the bicuspid, or pointed upper incisors, and semi-procumbent, pointed lower ones, characteristic of non-taeniolabidoid multituberculates were used for picking-up and killing insects or other prey. In relation to the backward power stroke the low position of the condylar process was advantageous for most multituberculates. In extreme cases (Sloanbaataridae and Taeniolabididae), the adaptation for crushing hard seeds, worked against the benefit of the low position of the condylar process and a high condylar process developed. Five new multituberculate autapomorphies are recognized: anterior and intermediate zygomatic ridges; glenoid fossa large, flat and sloping backwards (forwards in rodents), arranged anterolateral and standing out from the braincase; semicircular posterior margin of the dentary with condylar process forming at least a part of it; anterior position of the coronoid process; and anterior position of the masseteric fossa. The postorbital process in those multituberculates studied is situated on the parietal and the orbit is very large.

Key words: Multituberculata, Mammalia, Cretaceous, masticatory musculature.

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Contents:

Introduction

The present paper is a continuation of our previous work (Kielan-Jaworowska & Gambaryan 1994) in which we reconstructed the postcranial musculature of Asian multituberculate mammals and discussed multituberculate habits in general.

Simpson (1926) provided the first reconstruction of the masticatory musculature in multituberculates, using the Late Jurassic plagiaulacoid *Ctenacodon* from North America. When Simpson wrote his paper, the method of inferring jaw movements in herbivorous fossil mammals by recognition of the leading and trailing edges of worn individual cusps (Greaves 1973; Cosata & Greaves 1981; see also Rensberger 1973) was not known. Applying this method, Gingerich (1977) demonstrated that in multituberculates the lower jaw moved backward (palinally) during the power stroke. Simpson (1926) reconstructed, however, the multituberculate masticatory musculature essentially on rodent lines, in which the lower jaw during the power stroke moves forwards (proally) (Hiiemae 1971; Weijs 1975, 1994, and many others; see also Krause 1982 for terminology of jaw movements). Simpson (1926) regarded the diprotodont marsupial *Bettongia* as the closest analogue of multituberculates, but *Bettongia* has the forward chewing power stroke (Parker 1977).

Turnbull (1970), in a comprehensive paper on the mammalian masticatory apparatus, briefly summarized the musculature in multituberculates on the basis of Simpson's work. Parker (1977), in relation to her study on *Bettongia*, discussed multituberculate masticatory musculature. She misinterpreted the shape of the worn crescents on the molar cusps, and concluded that the multituberculates had a forward power stroke.

Sloan & Van Valen (1965) briefly commented on attachments of some masticatory muscles in the Late Cretaceous eucosmodontid *Stygimys*, but did not illustrate the muscles. Sloan (1979) reconstructed the jaw musculature of the early Eocene ptilodontoid *Ectypodus*. He was aware of the backward chewing stroke of multituberculates and his reconstruction

(Sloan 1979: Fig. 3) differs from that of Simpson (1926: Fig. 7) of *Ctenacodon*. Gingerich's (1977) conclusion concerning the backward direction of the power stroke in multituberculates was fully confirmed by Krause (1982), who studied the dental function of a Paleocene ptilodontoid *Ptilodus*. Krause recognized the two cycles of mastication in *Ptilodus*: the slicing-crushing cycle, which occurred when the large lower premolar (p4) sliced orthally into food held by the fourth upper premolar (P4), and the second grinding cycle, during which the lower jaw was pulled backward when the molars were in occlusion, producing longitudinal striations on the molars. Krause concluded that multituberculates were omnivorous (see Landry 1970 for comparison with rodents). Krause also demonstrated that, unlike in therians, triconodonts, and docodonts (Crompton & Hiiemae 1970; Crompton & Sita-Lumsden 1970; Crompton 1974), there was no transverse component in the lower jaw movements in multituberculates.

Gingerich (1984), in a review article on mammalian phylogeny and form and function of mammalian teeth pointed out that multituberculates are exceptional among mammals in chewing backward. He concluded that multituberculates (Gingerich 1984: p. 16) 'evidently separated from modern mammals before the masseter-pterygoid complex of jaw muscles became associated with shearing occlusion'. If so, the masticatory musculature of multituberculates would not be completely homologous to that of the Theria. Hopson *et al.* (1989) described for the first time the multituberculate jugal which, unlike in other mammals, lies against the medial surface of the zygoma and was not exposed laterally. They commented on the masseter muscles in relation to the position of the jugal. Wall & Krause (1992) provided the first vector analysis of the multituberculate masticatory apparatus (in *Ptilodus*).

Bryant & Seymour (1990: p. 116) argued that: 'It is apparent that without closely related living taxa, much of the detailed reconstruction of the musculature in extinct vertebrates must remain extremely speculative'. We believe that if the surface of the fossil bones is excellently preserved, it may be possible to reconstruct the musculature, in particular the masticatory musculature with some degree of confidence (see also van der Klaauw 1963). Multituberculates do not have close relatives among the living mammals, which makes the musculature reconstructions difficult. Recognition of their backward chewing stroke, however, may serve as a tool for testing the reconstructions of the musculature. Because of backward direction of the power stroke one would expect in multituberculates a different organization of the chewing muscles than in therian mammals. A relatively reliable reconstruction of the masticatory musculature is possible, if in addition to excellent preservation of the bone surface, at least one skull with a complete lower jaw is available. In this paper we reconstruct the masticatory musculature in the two families of taeniolabidoid multituberculates (Eucosmodontidae and Taeniolabididae) on the basis of well preserved skulls associated with lower jaws from the Late

Cretaceous of Mongolia. Our reconstructions are based to a large degree on comparisons with the masticatory musculature of rodents.

No attempt at reconstruction of the facial and occipital musculature of multituberculates has ever been made. The facial musculature may be difficult or even impossible to reconstruct in fossil mammals, as the facial muscles (in contrast to masticatory muscles) do not leave obvious scars on the bones (Gambaryan 1989). Of the facial muscles we were able to reconstruct only m. buccinator. We were unable to reconstruct the occipital musculature, because on the available neck vertebrae (Kielan-Jaworowska & Gambaryan 1994) the muscle scars cannot be identified and all the available occipital plates are not adequately preserved.

Abbreviations. — We use the following abbreviations for museum collections: AMNH — American Museum of Natural History, New York; PIN — Palaeontological Institute, Russian Academy of Sciences, Moscow; PU — Princeton Collection of Yale University, New Haven; USNM — United States National Museum, Washington; ZIN — Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Other abbreviations: ant. — anterior; interm. — intermedia; m. — muscle; med. — medialis; p. — pars; super. — superficialis.

Material and methods

The material used in this study derives from the Late Cretaceous (Djadokhta and Barun Goyot formations and their stratigraphic equivalents) of the Gobi Desert, Mongolia. The bulk of the material was collected during the Polish-Mongolian Palaeontological Expeditions (1963–1971), and is housed in the Institute of Paleobiology, Polish Academy of Sciences in Warsaw. The specimens from the same region housed in the Paleontological Institute of the Russian Academy of Sciences in Moscow have also been studied. We follow the age estimates of these formations by Gradziński *et al.* (1977): for the Djadokhta Formation and its stratigraphic equivalent Toogreeg beds — ?late Santonian and/or ?early Campanian; the Barun Goyot Formation and its stratigraphic equivalent the Red beds of Khermeen Tsav — ?middle Campanian. See, however, Fox (1978), Lillegraven & McKenna (1986) and Jerzykiewicz *et al.* (1993) for alternative age estimates.

We base our reconstructions of the musculature in the Eucosmodontidae primarily on *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974 and *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, using *Kryptobaatar dashzevegi* Kielan-Jaworowska 1970 for comparisons. The poorer quality of preservation of other eucosmodontid taxa occurring in the Late Cretaceous Gobi Desert formations, and of *Sloanbaatar mirabilis* Kielan-Jaworowska 1970, a member of the monotypic taeniolabidoid family Sloanbaataridae, did not allow reconstructions to be made. Our reconstruction
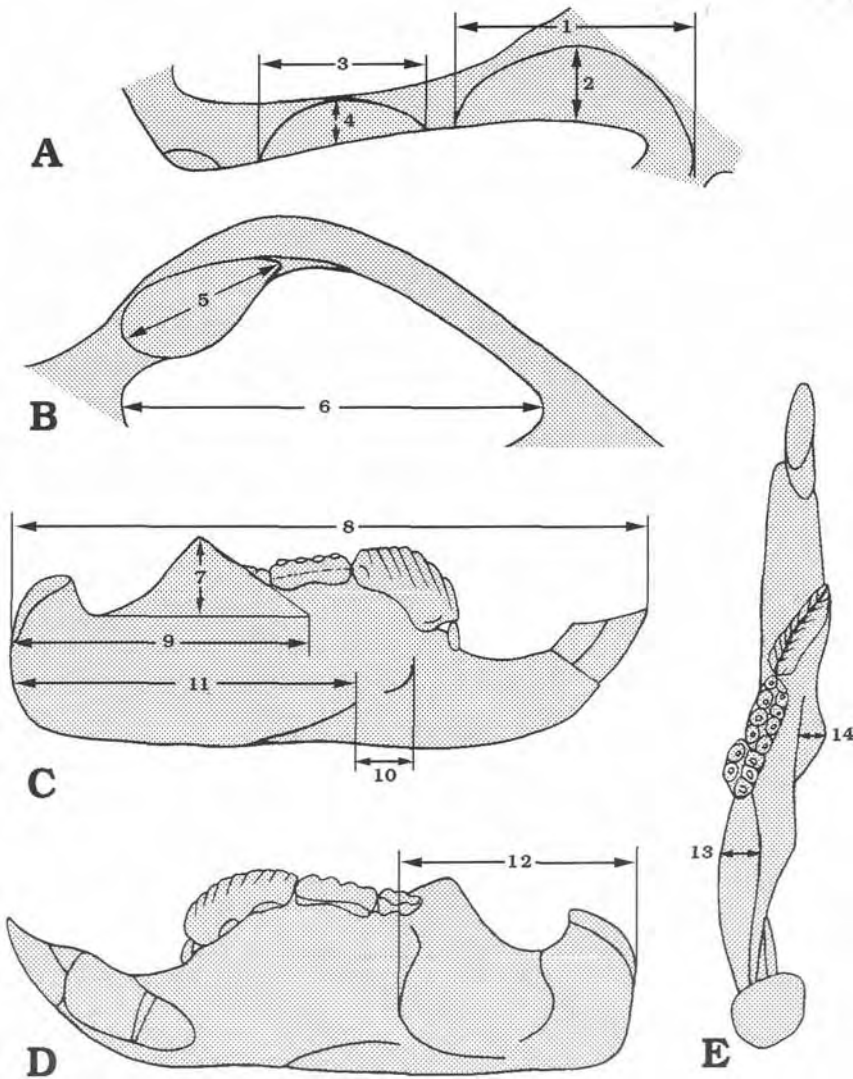
Fig. 1. Diagram showing distances for measurements (based on *Nemegtbaatar*, ZPAL MgM-I/81). A–B. Lateral and ventral views of the zygomatic arch. C–E. Lateral, medial and dorsal views of the lower jaw. 1, 2 — length and height of the anterior zygomatic ridge; 3, 4 — length and height of the intermediate zygomatic ridge; 5 — length of the glenoid fossa; 6 — length of the zygomatic arch; 7 — height of the coronoid process; 8 — length of the lower jaw; 9 — distance between the posterior margin of the lower jaw and the anterior end of the coronoid process; 10 — length of the masseteric fovea; 11 — distance between the posterior margin of the lower jaw and the anterior margin of the masseteric crest; 12 — distance between the posterior margin of the lower jaw and the anterior margin of the pterygoid fossa; 13 — width of the pterygoideus shelf; 14 — width of the masseteric crest.

of the musculature in the Taeniolabididae is based on *Catopsbaatar catopsaloides* (Kielan-Jaworowska 1974) (see also Kielan-Jaworowska 1994), but we discuss also the pterygoid muscles of *Kamptobaatar kuczyn-*

skii Kielan-Jaworowska 1970. *Nemegtbaatar* and *Chulsanbaatar* are from the Barun Goyot Formation and Red beds of Khermeen Tsav, *Catopsbaatar* is from the Red beds of Khermeen Tsav, while *Kryptobaatar*, *Kamptobaatar* and *Sloanbaatar* are from the Djadokhta Formation. As all the studied taxa belong to the monotypic genera, for the sake of brevity we shall use only the generic names.

In modern mammals, if there is a distinct ridge on the skull, the aponeurosis of a wide muscle originates on this ridge and the muscle fibres originate below it (Herring 1992). Although the particular portions of the fibres are differently oriented and take part in different jaw movements, the belly of the muscle as a whole is directed perpendicularly to the ridges (e.g., Evans & Christensen 1979, Fig. 6–13). The position of ridges helped us to reconstruct the direction of the muscles. The masticatory muscles in mammals usually are multipennate and have many functions (Herring 1979), however, we discuss only the most general function of the muscles, related to the backward and usually bilateral jaw movements (Krause 1982; Wall & Krause 1992). When the ridges or protuberances were hardly discernible, we reconstructed the relevant muscles only in cases, when the ridges were present in exactly the same places in more than one specimen, or at least in both dentaries. We discuss the methods of establishing the vectors on p. 68.

For comparative purposes we studied the skulls and musculature of several extant mammals. As the multituberculate skull superficially resembles that of rodents, in spite of basic difference in the directions of the power stroke, we have chosen the rodents as the main reference point. We examined the masticatory musculature of the rodents *Nannospalax nehringi*, *Rattus norvegicus*, and different species of the Microtinae and Dipodidae, but we figure here only that of *Ellobius lutescens*.

Bone surface

The cranial anatomy of the taxa studied here has been described by Kielan-Jaworowska (1970, 1971, 1974), Kielan-Jaworowska & Sloan (1979), Kielan-Jaworowska *et al.* (1986), Hopson *et al.* (1989), and Hurum (1992, 1994). In those descriptions, some, but not all ridges, protuberances and fossae on the skulls and lower jaws, related to the attachment of muscles were named. Below we describe these structures, and if not stated otherwise, the description is based on *Nemegtbaatar*.

Skull (Fig. 2). — Kielan-Jaworowska (1971) designated the ridge on the anterior part of the zygomatic process of the maxilla in *Kamptobaatar* and *Sloanbaatar* the zygomatic ridge. We call this ridge the anterior zygomatic ridge (crista zygomatica anterior). It is very prominent in all the taeniolabidoid multituberculates studied by us (Fig. 2). To the rear of the anterior zygomatic ridge, there occur two less prominent ridges on the zygomatic arch. We name the second ridge, situated on the squamosal in front of the

Fig. 2. Multituberculate skulls in lateral views, stereopairs. □A. *Catopsbaatar catopsaloides* (Kielan-Jaworowska 1974), PIN 4537-5, × 1.4. □B. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, ZPAL MgM-I/81, × 2. □C. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, (with lower jaws in occlusion), PIN 4537-2, × 4. All form the ?middle Campanian, Red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia; coated with ammonium chloride. 1 — orbital ridge; 2 — postorbital process; 3 — temporal protuberance; 4 — lambdoidal crest; 5, 6, 7 — anterior, intermediate and posterior zygomatic ridges; 8 — masseteric fovea; 9 — masseteric crest.

glenoid fossa — the intermediate zygomatic ridge (crista zygomatica inter-media), and the very weak third ridge, situated at the most posterior part of the zygomatic arch, to the rear and above the posterior margin of the glenoid fossa — the posterior zygomatic ridge (crista zygomatica posterior). Zygomatic ridges occur also in Plagiaulacoidea and Ptilodontoidea. The prominent anterior and intermediate zygomatic ridges, on the zygomatic processes of the maxilla and squamosal respectively, are unique for multituberculates, and we regard the possession of them as a multituber-culate autapomorphy. In therian mammals if a ridge occurs, it is single and is placed on the jugal rather than on the maxilla or squamosal (e.g., in *Canis*, see Evans & Christensen 1979).

On the medial side of the zygomatic arch, above the jugal which in multituberculates lies entirely on the medial side of the arch (Hopson *et al.* 1989), the dorsal part of both the maxilla and the squamosal protrudes slightly medially, forming a weakly pronounced, rounded ridge. We name this ridge the medial zygomatic ridge (crista zygomatica medialis). Kielan-Jaworowska *et al.* (1986) called the ridge that in *Nemegtbaatar* extends vertically along the anterior part of the orbital wall the orbital ridge (crista orbitalis). Kielan-Jaworowska (1971) called a rounded small fossa antero-dorsal to this ridge, lying in the part of the roof of the anterior orbital area made by the frontal, the orbitonasal fossa (fossa orbitonasalis). The orbitonasal fossa is situated in *Nemegtbaatar* and other studied taenio-labidoid taxa, at the posterodorsal end of the large pocket-like structure, that forms the anterior extension of the orbital area. This pocket is roofed dorsally and laterally by the frontal, lacrimal and maxilla, and is open ventrally. Sloan (1979) referred to it (in a ptilodontoid *Ectypodus*) as a pocket in front of the orbit. We designate it the orbital pocket (theca orbitalis).

The postorbital process in Asian taeniolabidoid multituberculates is placed on the parietal and overhangs the lateral wall of the braincase. Below this process there extends a very weak, slightly posteroventrally-di-rected protuberance, which becomes more prominent ventrally. Kielan-Jaworowska *et al.* (1986: Fig. 20b) gave a notation 'ridge' to the ventral, prominent part of this protuberance in *Nemegtbaatar*. We call this pro-tuberance the temporal protuberance (torus temporalis). Extending poste-romedial from the postorbital process there is a faint parietal crest (Kie-lan-Jaworowska 1971), referred to also in mammals as a temporal line (linea temporalis) (Getty 1975; Schaller 1992). Kielan-Jaworowska (1971: p. 10) stated that these crests (lines): 'are hardly visible anteriorly, but become more distinct posteriorly where they meet to continue medially as a short, faint sagittal crest.' The lambdoidal crests in multituberculates (Kielan-Jaworowska 1971: p. 10): 'are faint medially and together form a gentle arc which is convex anteriorly. Laterally, the lambdoidal crests become convex posteriorly, very prominent and crescent-shaped.' The lambdoidal crest continues anteroventral as the dorsal margin of the zygomatic process.

Fig. 3. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974. Lower jaw of the specimen in Fig. 2B, in medial (A) and lateral (B) views; stereopairs × 3, coated with ammonium chloride. 1 — symphysis; 2 — pterygoid fossa; 3 — transversal elevation; 4 — pterygoid fovea; 5 — lunule; 6 — temporal groove; 7 — masseteric fovea; 8 — masseteric crest; 9 — masseteric line; three, not numbered arrows in B denote (from front to back) the anterior, posterodorsal and posteroventral elevations.

Lower jaw. — Lateral side (Figs 2C, 3B, 4). The coronoid process is low in *Nemegtbaatar*, but high in other multituberculates (see, e.g., Fig. 17), and in all of them it is placed more anteriorly with respect to the length of the lower jaw than in all therian mammals, even more anteriorly than in rodents and small herbivorous marsupials (Table 4 and Fig. 12). We regard the anterior position of the coronoid process as a multituberculate auta-pomorphy. Anteroventral to the base of the coronoid process and along the medial side of its most anterior part, there extends a small, longitudinal groove, which we name the temporal groove (sulcus temporalis). Above this groove and below the bases of p4, m1 and the anterior part of m2 there is a half-moon shaped convexity which we name the lunule (lunula).

Extending from the ventral end of the condylar process, all along the posterior and ventral margins of the dentary is a sharp masseteric line

(Evans & Christensen 1979), which anterodorsally passes into the masseteric crest. The term masseteric crest has been employed for multituberculates in two different meanings. For example in Simpson's (1926) and Hahn's (1978) sense, the masseteric crest incorporates both the prominent part that extends across the lateral surface of the dentary, as the anteroventral margin of the masseteric fossa, and the posterior prolongation of this crest, that extends along the ventral margin of the dentary (masseteric line in our terminology). Sloan & Van Valen (1965), Kielan-Jaworowska (1971) and others employed the term masseteric crest only for the anteroventral prominent margin of the masseteric fossa. We follow this latter usage (number 9 in Fig. 2C and number 8 in Fig. 3B). Sloan & Van Valen (1965) recognized in *Stygimys* two masseteric crests (see below). Ride (1957) called the masseteric crest in *Plagiaulax* the masseteric shelf. The masseteric crest (masseteric ridge) occurs also in some rodents (e.g., Greene 1935; Weijs 1973; Kesner 1980), and in diprotodont marsupials (Abbie 1939). Kesner (1980) writes about the dorsal and ventral masseteric crests in microtine rodents, and only the ventral one corresponds to the masseteric crest of other authors. The masseteric crests in multituberculates and therians are, however, not homologous in the musculature that inserts upon them. In Theria, the masseteric crest is site for insertion of masseter lateralis profundus pars anterior, while in multituberculates, according to our interpretation (Fig. 6) it is masseter superficialis pars anterior that inserts upon it.

The masseteric fossa in multituberculates is situated more anteriorly than in all therian mammals, and we regard its anterior position as a multituberculate autapomorphy. In front of the masseteric crest, and slightly ventral to it there is a shallow rounded fovea, which we designate the masseteric fovea (fovea masseterica) (number 10 in Fig. 1). The masseteric fovea is delimited anteroventrally by a small, rounded ridge. In most genera this ridge is weakly pronounced, but is prominent, for example, in *Chulsanbaatar* (Fig. 2C) and *Stygimys* (Sloan & Van Valen 1965: Fig. 4). Sloan & Van Valen referred to it as a 'more forward' of two masseteric crests. The anterior margin of the masseteric fovea is placed in multituberculates more anteriorly than the anterior margin of insertion of the masseteric muscles in all therian mammals (Table 4 and Fig. 12). In studied multituberculates this fovea is best defined in *Chulsanbaatar* (number 8 in Fig. 2C), where it forms a distinct pit, while in *Nemegtbaatar* it is very shallow. In *Kryptobaatar* the masseteric fovea is situated dorsal to the anterior part of the masseteric crest and is confluent with the masseteric fossa.

Between the masseteric line and the base of the coronoid process the surface of the bone is undulating. We recognize, albeit tentatively, on this surface three, very weakly pronounced elevations (arrows in Fig. 3B), called anterior elevation (eminentia anterior), posterodorsal elevation (eminentia posterodorsalis) and posteroventral elevation (eminentia posteroventralis).
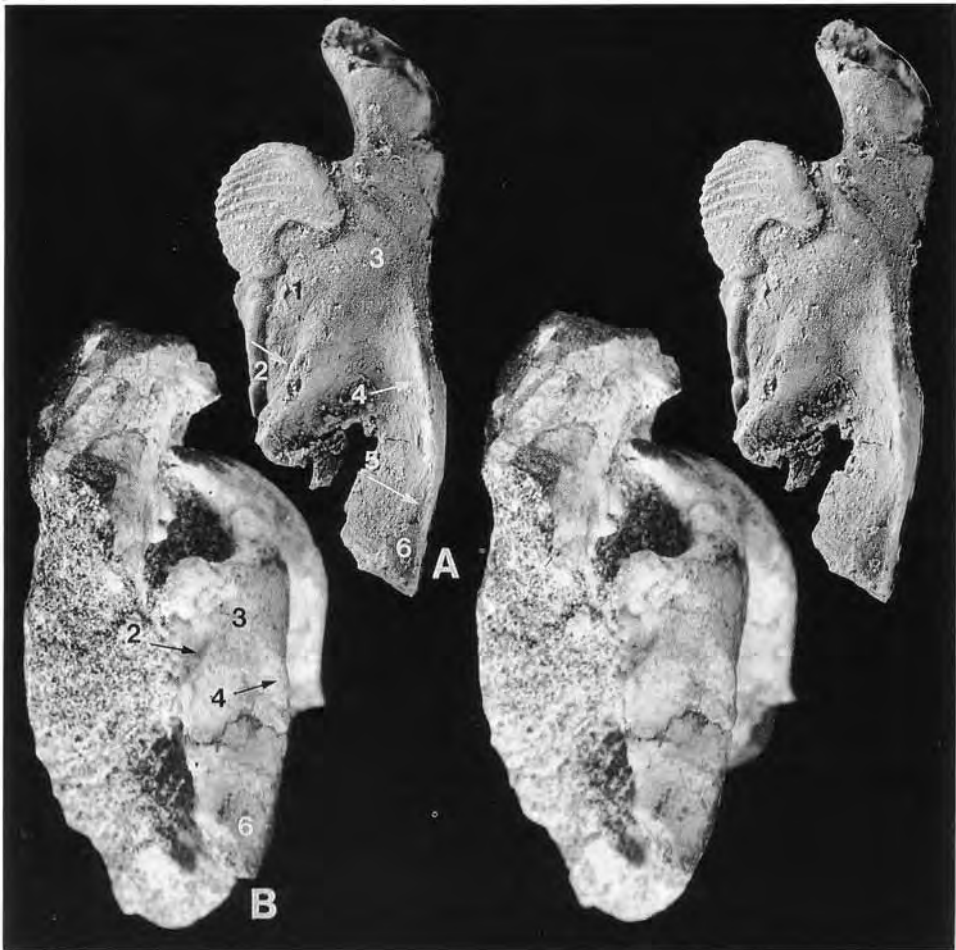
Fig. 4. ▢A. Lateral view of the partial lower jaw of *Ectypodus szalayi* Sloan 1981, AMNH 35533, stereopair × 7, coated with ammonium chloride. Paleocene, Gidley Quarry, San Juan Basin, New Mexico. ▢B. Lateral view of the snout associated with partial lower jaws of *Kryptobaatar dashzevegi* Kielan-Jaworowska 1970, ZPAL MgM-I/53, stereopair × 4. ?late Santonian and/or early Campanian, Bayn Dzak, Gobi Desert, Mongolia. 1 — lunule; 2 — temporal groove; 3 — masseteric fovea (situated in both taxa within the anterior part of the masseteric fossa); 4 — masseteric crest; 5 — masseteric line; 6 — insertion area for masseter superficialis p. posterior.

Medial side (Fig. 3A). The pterygoid fossa is very deep, its anterior border is convex anteriorly, situated below the posterior margin of m2. Ventrally this border is developed as a crest that continues posteriorly as the margin of the horizontal floor of the pterygoid fossa. It has been named by Simpson (1926) the pterygoid crest; we follow Miao (1988, 1993) in calling it the pterygoideus shelf. The pterygoid fossa is limited posteriorly by the subvertical elevation, convex posteriorly, to the rear of which there is another, less deep fossa, which we call the pterygoid fovea (fovea

pterygoidea). Dorsally the pterygoid fossa is limited by the longitudinally directed elevation, which we name the transversal elevation (eminentia transversalis). The posterior margin of the dentary, below the condylar process is developed as a sharp marginal ridge, similar to the masseteric line on the lateral side.

Myological reconstructions

As summarized by Hiiemae & Jenkins (1969) the terminology of the masticatory musculature in mammals and in particular in rodents is not unified. In therian mammals (see, e.g., Getty 1975; Saban 1968; Turnbull 1970; Evans & Christensen 1979; Schaller 1992) m. masseter consists of two or three layers, referred to (in case of only two layers) as superficial and deep (e.g., in the goat and ox), or (in case of three layers) as superficial, middle and deep (e.g., in sheep, dog, and in man; see also Davies & Davies 1962). In rodents m. masseter is separable into three layers, two of which are separable again into two parts. Tullberg (1899), in his classical monograph of rodents, divided m. masseter into masseter lateralis (with portio superficialis and portio profundus) and masseter medialis. Hill (1937) listed synonyms of the parts of the masseter in rodents. He generally adopted Tullberg's division, treating, however, two 'portios' of masseter lateralis as separate layers. As a result, in Hill's division, m. masseter is separable into three layers: masseter superficialis, masseter lateralis profundus (divided into pars anterior and pars posterior) and masseter medialis (divided into pars anterior and pars posterior). Hill's division has been followed by many (e.g., Rinker 1954; Klingener 1964) and has been extensively used in the Russian anatomical literature (e.g., Gambaryan *et al.* 1980; Vorontsov 1982 and references therein). However, Turnbull (1970) and Weijs (1973) among others, followed Schumacher (1961) in dividing m. masseter into superficial masseter and deep masseter with anterior and posterior parts, recognizing in addition m. zygomaticomandibularis, with infraorbital, anterior, and posterior parts. M. zygomaticomandibularis corresponds to masseter medialis of Tullberg (1899) and Hill (1937). We follow Hills' division of the masticatory musculature in rodents (Fig. 5), and we employ it for multituberculates.

The adoption of the rodent masticatory terminology for multituberculates does not necessarily imply homology. As, however, the evident muscle scars preserved on the studied skulls indicate the presence of three layers of the masseter muscle, and as other details of the masticatory musculature are also similar to those of rodents, we regard it reasonable to apply the rodent masticatory terminology in our descriptions. In monotremes m. masseter is also separable into three layers (Schulman 1906; Edgeworth 1935; Saban 1971), but because of their different dietary specialization, and limited range of the lower jaw movements, they could not serve as a model for comparisons with multituberculates. The multituberculate mas-
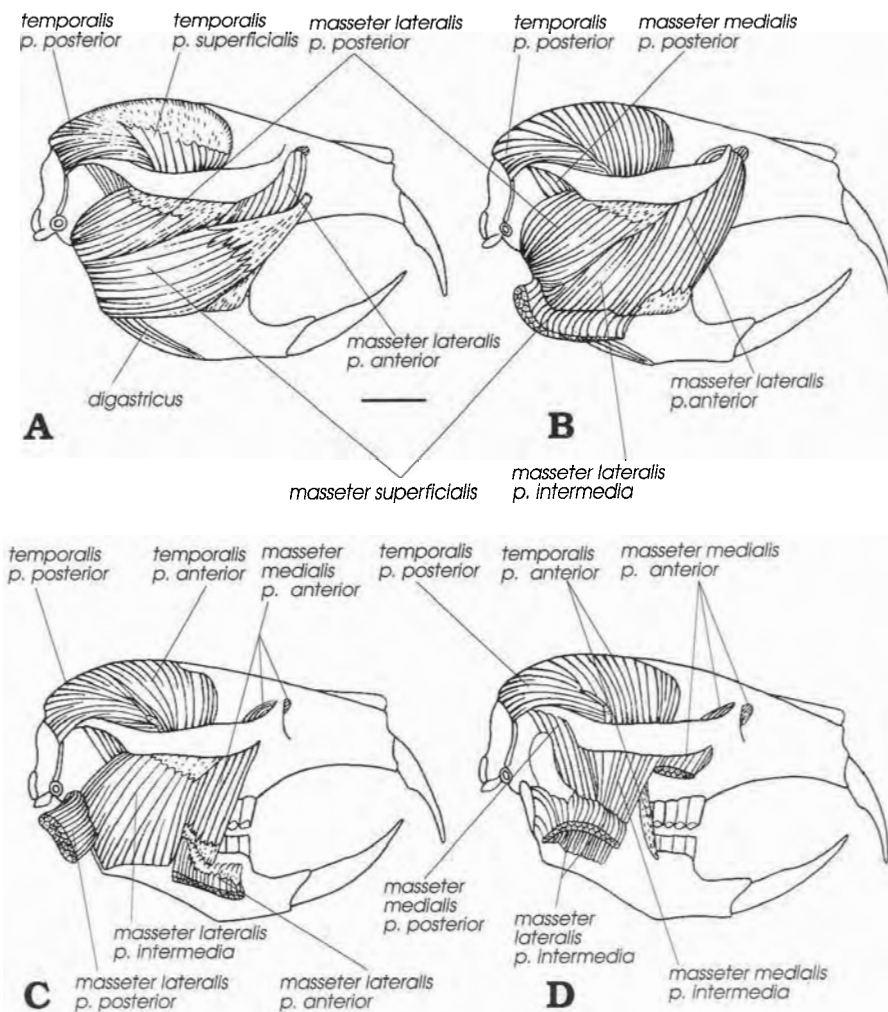
Fig. 5. Masticatory musculature in extant myomorph rodent *Ellobius lutescens*. A–D. Superficial, second, third and deep layers respectively. Masseter lateralis profundus is referred to as masseter lateralis. Scale bar — 5 mm.

ticatory musculature appeared many millions of years earlier than that of rodents, e.g., possibly 160 million years earlier if it developed in the earliest known (Rhaetian) multituberculate *Mojo* (Hahn *et al.* 1987), and 85 million years earlier if it developed as late as in the Kimmeridgian multituberculates (Hahn 1978, 1987, 1988 and references therein). It is therefore plausible to assume that the multituberculate pattern of the masticatory musculature originated independently from that of rodents.

Eucosmodontidae (*Nemegtbaatar*) (Figs 2B, 3, 6, 8–11, 12G, 14F, 15A, 17D, 19). — M. masseter in *Nemegtbaatar* and in other multituberculates was (as in rodents) apparently separable into three layers: masseter superficialis, masseter lateralis profundus, and masseter medialis.

Masseter superficialis (Figs 6, 8). Although in extant mammals masseter superficialis is not separable (e.g., Fig. 5A, B), the presence of two distinct zygomatic ridges in multituberculates allows us to reconstruct masseter superficialis as separable into pars anterior and pars posterior. Pars anterior in *Nemegtbaatar* originated from the anterior zygomatic ridge, converged ventrally and inserted on the masseteric crest, well developed in *Nemegtbaatar* and *Chulsanbaatar* (Figs 2C, 3B). The anterior zygomatic ridge in *Nemegtbaatar* in lateral view forms an arch convex dorsally; the perpendiculars sent from this ridge meet at the masseteric crest.

Masseter superficialis pars posterior originated from the intermediate zygomatic ridge, well preserved in *Nemegtbaatar* and *Chulsanbaatar* (Fig. 2B, C) and inserted on and above the masseteric line of the dentary (Figs 2C, 3). This insertion area is less clear in *Nemegtbaatar* than that of the pars anterior. We recognize this insertion on the basis of perpendiculars sent ventrally from the arch of the intermediate zygomatic ridge, and on comparisons with *Kryptobaatar* and *Ectypodus* (Fig. 4), where at the posteroventral margin of the dentary there is an elongated flat area, apparently for the insertion of this muscle.

Masseter lateralis profundus is reconstructed by us as a wide muscle, similar to that occurring in most extant mammals. It originated from the whole ventral surface of the zygomatic arch, between the anterior margin and the glenoid fossa and inserted on a large area on the ventral part of the dentary, having its aponeurosis along the masseteric line, with the muscular part laying above it. The extent of the origin of the muscular part is tentative. We base this reconstruction on the fact that in all mammals, in which m. masseter consists of three layers, there is an extensive masseter lateralis profundus situated between masseter superficialis and masseter medialis.

Masseter medialis in rodents is separable into three parts (Fig. 5, and e.g., Gambaryan *et al.* 1980; Vorontsov 1982) and we suggest that in multituberculates this muscle was similarly separable into pars anterior, pars intermedia and pars posterior (Figs 6, 8). Pars anterior originated in *Nemegtbaatar* from the anterior part of the medial wall of the orbital space: from a well developed orbital ridge and a relatively large orbital pocket. It inserted on the masseteric fovea in front of the masseteric crest. The origin of this muscle has been similarly reconstructed by Sloan (1979) for *Ectypodus* (see Fig. 13B and discussion on p. 67). This muscle rarely originates within the orbital pocket in therian mammals, but it does, for example, in some hystricomorph rodents, e.g., Bathyergidae (Boller 1970), and in extinct South American marsupials the Argyrolagidae (Simpson (1970).

We reconstruct masseter medialis pars intermedia in *Nemegtbaatar* as differentiated into two bellies. Both originated from the medial zygomatic ridge, and inserted on the weak anterior and posterodorsal elevations. The reconstruction of the division of this muscle into two bellies in *Nemegt-*
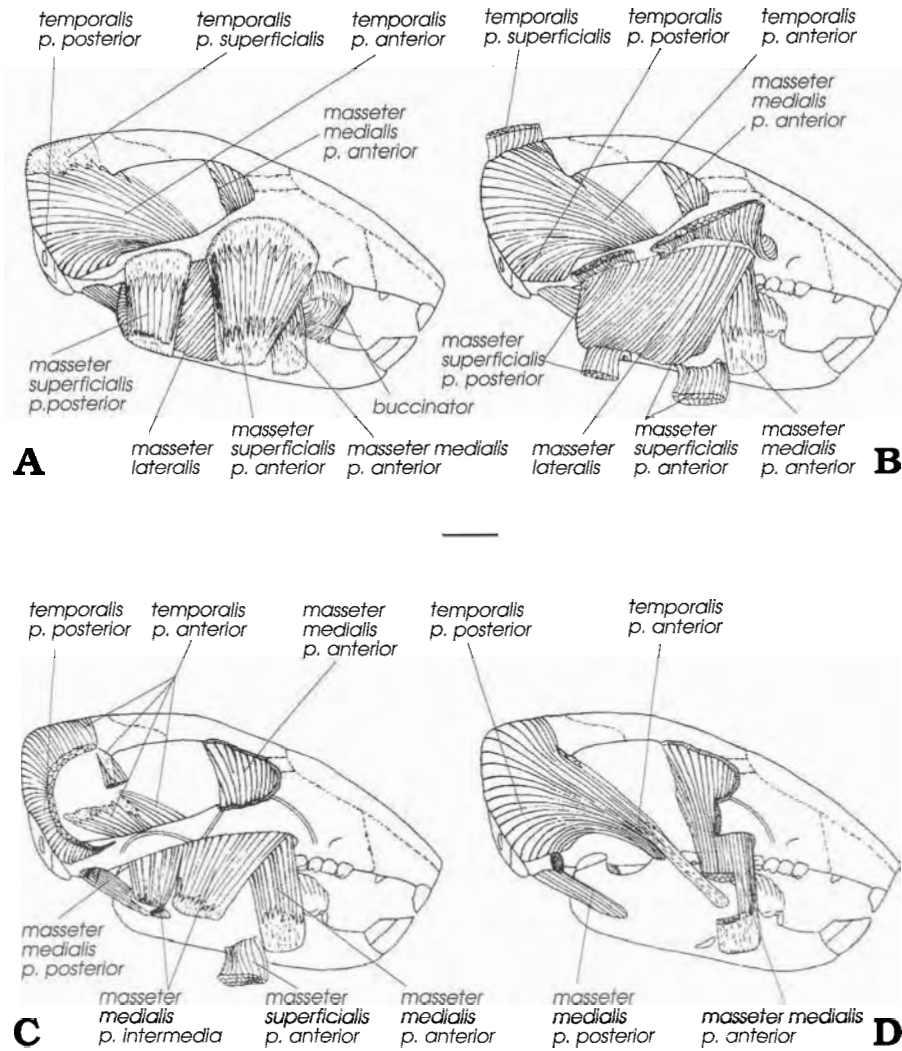
Fig. 6. Reconstruction of the masticatory musculature in *Nemegtbaatar gobiensis*, based on the surface topography of the bones. A–D. Superficial, second, third and deep layers respectively; in C and D parts of the frontal, lacrimal and maxilla have been removed to show insertion of masseter medialis p. anterior in the orbital pocket. In D zygomatic arch has been removed. Masseter lateralis profundus is referred to as masseter lateralis. Scale bar — 5 mm.

baatar is largely hypothetical, based only on the presence of two separate weak elevations on the dentary. Pars posterior originated from the posterior zygomatic ridge (situated to the rear of the glenoid fossa) and inserted on the posteroventral elevation on the dentary. Whereas the place of origin of this muscle can be well established, its insertion on the dentary is hypothetical.

M. temporalis (Figs 6, 8) consisted in *Nemegtbaatar* of three parts, as in most modern mammals: pars superficialis, pars anterior and pars

posterior. Pars superficialis in extant mammals usually originates by an aponeurosis from the parietal bone below the temporal line and sagittal crest. From the surface of this aponeurosis most of the muscular fibers of pars superficialis take their origin. Ventrally they pass into the tendon, which may insert in various places on the buccal wall of the dentary (Turnbull 1970). In *Nemegtbaatar* (and in all other studied multituberculates) there existed also pars superficialis, which originated as in extant mammals and inserted by a tendon in the temporal groove of the dentary. Pars anterior apparently originated from a very large area: from the entire surface of the parietal bone, under the aponeurosis of pars superficialis, from the postorbital process and temporal protuberance below it, and from the anterior part of the anterior lamina of the petrosal. The rugose surface of the ventral side of the postorbital process and of the ventral part of the temporal protuberance indicates the presence of an aponeurosis. Pars anterior possibly inserted by a common tendon with pars superficialis in front of the coronoid process. We reconstruct pars posterior originating, as in modern mammals, from the lambdoidal crest, the posteroventral part of the parietal and the anterior lamina of the petrosal. Extending posteriorly from the ventral margin of the temporal protuberance toward the lambdoidal crest, there is a slightly rugose convexity, possibly for the aponeurosis (and ventral margin) of pars posterior. Pars posterior inserted on the medial and lateral sides of the coronoid process (Figs 3, 4).

M. pterygoideus (Fig. 8). We recognize in *Nemegtbaatar* (as in most extant mammals) two muscles: m. pterygoideus medialis and m. pterygoideus lateralis. The choanal region in multituberculates differs from that in extant mammals in the position of the pterygoids, which do not form the lateral walls of the choanae, but are situated between the vomer and the alisphenoids. Because of this, the choanae are divided by the vomer and pterygoids into four channels (Kielan-Jaworowska 1971). From the lateral channel, between the pterygoid and the alisphenoid, the posterior part of which forms the prominent alisphenoid ridge (Kielan-Jaworowska 1971: Pl. 1: 2b and Pl. 2), originated m. pterygoideus medialis. M. pterygoideus medialis inserted in multituberculates in the large pterygoid fossa delimited dorsally by the transversal elevation (Figs 3A, 8) and on the extensive pterygoideus shelf. The pterygoid fossa is placed in multituberculates more anteriorly than in extant therian mammals, where it occupies the most posteroventral part, including the angular process of the dentary.

The origin of m. pterygoideus lateralis is clearly seen in *Kamptobaatar* (Kielan-Jaworowska 1971: Pl. 1: 2a), in which on the anterolateral side of the alisphenoid ridge, there is a concave area that extends along the alisphenoid to the posterior part of the maxilla, to the rear of M2, and passes posteriorly on the anteroventral part of the anterior lamina of the petrosal. In *Nemegtbaatar*, where it is less clear, it might originate similarly as in *Kamptobaatar*. Pterygoideus lateralis inserted in the pterygoid fovea, well preserved in the lower jaws in *Nemegtbaatar* (Fig. 3A).

M. digastricus (this muscle may be detrahens mandibulae as in mono- tremes). The area of origin of this muscle is not obvious in available materials of *Nemegtbaatar*, *Kryptobaatar* and *Chulsanbaatar*. It possibly inserted on the medial side of the dentary posteroventral to the symphysis. The area of its insertion is poorly preserved in *Nemegtbaatar*, but it is reconstructed in Fig. 8.

One part of m. *buccinator* is reconstructed as originating from the lateral side of the maxillary bone, above the alveoli of p3–m2, and the other part of this muscle from the lunule (Figs 3B, 4A, 6A, 8) on the dentary. It apparently attached at the intermediate tendon, as in extant mammals.

Other Eucosmodontidae (Figs 2C, 4B, 7A, 12H). — *Chulsanbaatar* (Figs 2C, 7A, 12H) differs from *Nemegtbaatar* in having a relatively higher and longer anterior zygomatic ridge; in *Chulsanbaatar* its length and width amount to 73% and 15% of the length of the zygomatic arch respectively, in *Nemegtbaatar* 68% and 21%. The intermediate zygomatic ridge is also slightly longer (42% of the length of the arch in *Chulsanbaatar*, against 35% in *Nemegtbaatar*), and has the same relative height (12% of the length of zygomatic arch) in both taxa. The intermediate zygomatic ridge is situated closer to the anterior one than in *Nemegtbaatar*. The masseteric crest is more prominent and longer in *Chulsanbaatar* (Fig. 2C, and Kielan-Jaworowska 1974: Pl. 17: 1a). In *Chulsanbaatar* (Fig. 2C, and Kielan-Jaworowska 1974: Pl. 16: 1e) the masseteric fovea is relatively deeper, situated more ventrally than in *Nemegtbaatar* and surrounded anteroventrally by a prominent ridge. This formed the insertion area for the superficial aponeurosis of masseter medialis pars anterior, more strongly developed than in *Nemegtbaatar*. In *Nemegtbaatar* it was im- possible to recognize the place of insertion of masseter superficialis posterior, however, in *Chulsanbaatar*, close to the posteroventral margin of the lower jaw, dorsal to the masseteric line, there extends a small elevation, which divided the insertion areas of the masseter superficialis pars posterior (below it) and masseter lateralis profundus (above). We were unable to recognize the posterior and anterior elevations on the lower jaws of *Chulsanbaatar*, tentatively recognized in *Nemegtbaatar* as the insertion areas of the two bellies of the masseter medialis pars intermedia. The area of origin of m. digastricus is poorly preserved in *Chulsanbaatar* (as in *Nemegtbaatar*), but recognizable (Kielan-Jaworowska 1974: Pl. 14: 1d).

In *Chulsanbaatar* m. temporalis was larger than in *Nemegtbaatar*, as the horizontal distance between the postorbital process and the lambdoi- dal crest amounts to 54% of the length of the zygomatic arch, and in *Nemegtbaatar* 45%.

Among the *Kryptobaatar* specimens in the ZPAL collection the zygomatic arch (right) has been preserved only in ZPAL MgM-I/41 (Kielan-Jaworow- ska & Gambaryan 1994: Fig. 1C–F). All three zygomatic ridges were somewhat distorted and have not been measured. Other details of skull structure related to muscular attachments could not be observed. In *Kryptobaatar* (Fig. 4B) the masseteric fovea lies dorsal to the masseteric

crest and is confluent with the anterior part of the masseteric fossa. On this basis we speculate that in *Kryptobaatar* masseter superficialis pars anterior covered the posterior part of the insertion of the masseter medialis pars anterior, as we have found also in the ptilodontoid *Ectypodus* (Fig. 4A).

In non-Asian eucosmodontids, fragments of the skull have been preserved in *Stygimys*, in which a very strong anterior zygomatic ridge is present (Sloan & Van Valen 1965: Fig. 4). These authors stated (Sloan & Van Valen 1965: p. 223) that in *Stygimys*: 'The superficial masseter originates on the zygomatic process of the maxilla and inserts on the more forward crest, the deep masseter inserts on the more posterior crest and probably extended at least partially, through the infraorbital foramen to originate on the facial portion of the maxilla. This modification parallels that of the hystricomorph and caviomorph rodents'. The 'more forward crest' of Sloan & Van Valen (1965) corresponds to the anteroventral prominent margin of the masseteric fovea in our terminology. We reconstruct m. masseter medialis pars anterior as inserting upon it. We do not see any reason to believe that in the taeniolabidoids studied by us masseter medialis pars anterior (deep masseter of Sloan & Van Valen 1965) extended through the infraorbital foramen.

Sloanbaataridae (Fig. 17D). — *Sloanbaatar* differs from the studied Eucosmodontidae in having the zygomatic arches more expanded laterally, and both anterior and intermediate zygomatic ridges more gracile and relatively shorter and lower. The lower jaw differs from that of the above described Eucosmodontidae in having the lower margin arranged at an angle of 30° with respect to the occlusal surface of the teeth (11° in *Nemegtbaatar*) and in having the condylar process facing more dorsally and placed high above the occlusal level of the molars, rather than at about this level. The coronoid process is small and flared laterally and the masseteric fovea distinct and delimited anteriorly by a ridge situated below the anterior root of p4, indicating the presence of a powerful masseter medialis pars anterior. Otherwise the bone surface in the only known skull of *Sloanbaatar* (Kielan-Jaworowska 1970: Pl. 10: 22, Pls 12, 13; 1971: Pl. 5; Kermack & Kielan-Jaworowska 1971: Pl. 1) is cracked and does not allow the reconstruction of other muscles.

Taeniolabididae (Figs 2A, 7B, 17B). — In *Catopsbaatar* the zygomatic arch is deeper and shorter than in the studied Eucosmodontidae. The anterior zygomatic ridge is arranged as in the Eucosmodontidae, and the area of origin of the masseter superficialis pars anterior is proportionally much larger; its length is 77% of the length of the zygomatic arch, the height is almost twice as great as in the Eucosmodontidae and amounts to 45% of the length of the zygomatic arch. The surface on the zygomatic arch, embraced dorsally by the anterior zygomatic ridge is in lateral aspect slightly concave. The orbital pocket is in *Catopsbaatar* relatively larger than in any studied multituberculate and the eyes were situated very far posteriorly (Kielan-Jaworowska 1974: Pls 18, 19; Kielan-Jaworowska & Sloan 1979: Fig. 1; Figs 2A, 7B, and 17B in this paper).
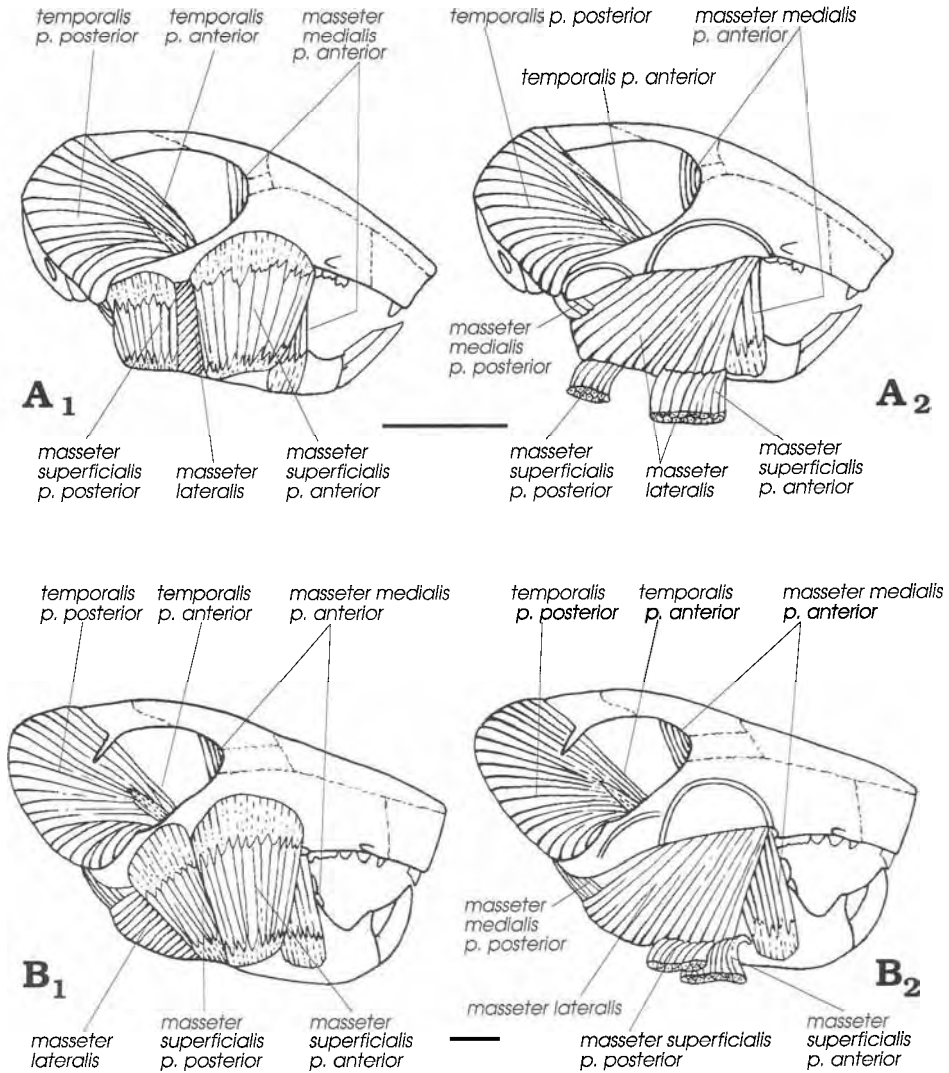
Fig. 7. Reconstruction of the masticatory musculature. □A *Chulsanbaatar vulgaris*. □B. *Catopsbaatar catopsaloides*, based on surface topography of the bones. A$_1$, B$_1$ superficial layers. A$_2$, B$_2$ second layers. Masseter lateralis profundus is referred to as masseter lateralis. Scale bars — 5 mm.

In the holotype (and in other not figured specimens) of *Catopsbaatar catopsaloides* (referred to originally as *Djadochtatherium*) in ZPAL collection, the lower jaws are abraded and the masseteric crest and the ridge in front of the masseteric fovea are not very prominent (Kielan-Jaworowska 1974: Pl. 17: 2; Pl. 20: 1). In the fragmentary lower jaw examined by us (PIN 4537-5, not figured) the masseteric crest is very prominent and the

masseteric fovea is delimited anteriorly by a rounded ridge, as prominent as in *Chulsanbaatar*. This indicates that masseter superficialis pars anterior was very strong, which is correlated with a large orbital pocket. The intermediate zygomatic ridge in *Catopsbaatar* is differently arranged than in *Nemegtbaatar*, forming in lateral view an arch directed posteroventrally, rather than being more symmetrical and convex dorsally as in *Nemegtbaatar* and *Chulsanbaatar* (Fig. 2). Its length amounts to 40% of the length of the zygomatic arch, the height 18%, which is 1.5 times higher than in the Eucosmodontidae. The two ridges are situated in *Catopsbaatar* closer to one another than in *Nemegtbaatar*. The position of the ridges shows that masseter superficialis pars anterior and pars posterior apparently converged ventrally, possibly pars posterior was in part covered laterally by pars anterior. It may be inferred from the position of their origins that these muscles inserted together on the masseteric crest (Fig. 7B). The anterior, posterodorsal and posteroventral elevations on the lateral side of the lower jaw, recognized tentatively in *Nemegtbaatar* (Figs 3B, 8) are not recognized in *Catopsbaatar*.

Kielan-Jaworowska (1971) described in the taeniolabidid *Kamptobaatar* an orbitonasal fossa in the posterior part of the roof of the orbital pocket (in the frontal bone), and interpreted it as housing a gland. In *Sloanbaatar* there are two such fossae to the rear of the orbital ridge, the posterior one smaller. Because of the poor state of preservation of studied *Catopsbaatar* skulls we could not recognize such fossae. Our reconstruction of the origin of masseter medialis pars anterior in the orbital pocket in *Catopsbaatar* (and in other Asian Taeniolabidoidea) does not preclude the possibility that these fossae were related to glands.

The coronoid process in *Catopsbaatar*, and in other Taeniolabididae (Fig. 17B, see also Granger & Simpson 1929; Jepsen 1940; Miao 1988) is higher than in the studied Eucosmodontidae. This indicates a stronger development of m. temporalis than in the Eucosmodontidae. The postorbital process is relatively very long in *Catopsbaatar* (Kielan-Jaworowska 1974: Pl. 18: 1c), which indicates a more powerful m. temporalis pars anterior than in the Eucosmodontidae. In extant mammals in which the postorbital process is long (e.g., in *Canis*), m. temporalis originates from its posterior and ventral surface, from the very end of the process originates the orbital ligament (Evans & Christensen 1979). It seems probable that this was also the case in *Catopsbaatar*. *Catopsbaatar* displays the pattern of musculature generally similar to that of the Eucosmodontidae, however, it had a more powerful masticatory muscles. The origin of the pterygoid muscles is not recognizable in *Catopsbaatar*, but has been recognized in *Kamptobaatar*, discussed on p. 60.

In the specialized Paleocene taeniolabidid *Lambdopsalis* the zygomatic arches have not been preserved (Miao 1988). The complete right zygomatic arch of *Taeniolabis* (Broom 1914: Pl. 12, upper photograph), shows the prominent anterior and intermediate zygomatic ridges. The posterior zygomatic ridge is less obvious, but possibly present. The lower jaw in

Taeniolabis is relatively short, with an unusually strong masseteric crest, forming a wide shelf (Granger & Simpson 1929). In both *Lambdopsalis* and *Taeniolabis* the anterior margin of the orbit and the postorbital process are situated more anteriorly than in *Catopsbaatar* and in other Asian Cretaceous Taeniolabidoidea. The orbital pocket characteristic of studied Asian genera (and also of *Ectypodus*; Sloan 1979) was present in *Lambdopsalis*, but reduced in size (Desui Miao, personal communication, December 1994). Sloan (1981) stated that the pocket is present in *Taeniolabis taoensis* (AMNH 16321) and that this part of the skull was erroneously reconstructed by Broom (1914) and Granger & Simpson (1929). The skulls of *Lambdopsalis* and *Taeniolabis* differ from the studied Asian genera in having the prominent sagittal and lambdoidal crests. The coronoid process in *Lambdopsalis* is relatively high and flares laterally (as in *Sloanbaatar*), while in *Taeniolabis* it has not been completely preserved and was reconstructed by Granger & Simpson (1929) as relatively very high.

Most of the differences between specialized taeniolabidids (*Lambdopsalis* and *Taeniolabis*) and Asian taeniolabidoid genera studied by us, are related to the acquisition of the gnawing function of the incisors in these specialized forms and development of a very strong m. temporalis. The primitive taeniolabidid *Catopsbaatar* studied by us, characterized by a very large orbital pocket and eyes situated far posteriorly, apparently does not lay on the evolutionary line leading to these advanced Paleocene taeniolabidids.

Plagiaulacoidea. — The plagiaulacoid Paulchoffatiidae (we follow Hahn 1993 in assigning the Paulchoffatiidae to the Plagiaulacoidea, contra Kielan-Jaworowska & Ensom 1992) from the Kimmeridgian or Oxfordian of Portugal (see Lillegraven & Krusat 1991 for discussion of the age) are the oldest multituberculates for which the skulls are known. None of the preserved skulls is complete, all are crushed and the bones surface is poorly preserved (Hahn 1969, 1977, 1978, 1985, 1987, 1988; Hahn & Hahn 1994). The anterior zygomatic ridge is present in *Paulchoffatia delgadoi, Kuehneodon dryas, Pseudobolodon oreas* and in several unidentified taxa. It is perhaps most prominent in Paulchoffatiidae, gen. et sp. indet. (Hahn 1985: Pl. 1: 4). In all the Paulchoffatiidae the anterior zygomatic ridge is situated more anteriorly and lower (below the infraorbital foramen) than in the Taeniolabidoidea. Behind it, in *Pseudobolodon oreas* there is a poorly preserved intermediate zygomatic ridge (Hahn 1985: Pl. 2: 1, 3a, 3b), placed on the zygomatic arch, and (if correctly recognized) situated more anteriorly than in the Taeniolabidoidea. The posterior zygomatic ridge and other structures related to muscular attachments have not been preserved in the Paulchoffatiidae (Gerhard Hahn, personal communication, April 1994), and the details of the structure of their orbital area are not known.

The shape of the paulchoffatiid lower jaws varies. In all of them the diastema is much shorter than in later multituberculates, the coronoid process is very large, with a wide base, and if completely preserved, e.g.,

in *Paulchoffatia delgadoi* (Hahn 1978: Pl. 4: 15, 16) it extends far posteriorly, almost to above the level of the condylar process, and the lower incisor is very robust. The masseteric fossa is deep and well defined in all the taxa and the masseteric crest is very prominent. In *Meketibolodon robustus*, referred to as *Pseudobolodon* (Hahn 1978: Pl. 1: 1b), there is a masseteric fovea in front of the masseteric fossa, recognizable also in *Kuehneodon dietrichi* (Hahn 1978: Pl. 2: 5a). In both taxa the fovea is situated higher than in *Nemegtbaatar* and much higher than in *Chulsanbaatar*. The fovea is less obvious in *Paulchoffatia delgadoi* (Hahn 1978: Pl. 4: 16b).

All the described skulls of the Allodontidae and Plagiaulacidae are fragmentary. The two partial skulls from the Morrison Formation, reported by Engelmann *et al.* (1990), showing limited enamel band on the lower incisors, are still to be described. Although the upper teeth are relatively well preserved in *Ctenacodon* and *Bolodon*, the zygomatic arch has not been preserved and the zygomatic ridges and other structures related to muscular attachments cannot be recognized (Simpson 1928, 1929; Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska & Ensom 1992). The lower jaw has been preserved in *Ctenacodon serratus*, *Plagiaulax becklesii* and *Zofiabaatar pulcher* (Simpson 1928, 1929; Ride 1957; Bakker & Carpenter 1990). All show a low condylar process, a high coronoid process and a large incisor or incisor alveolus. In *Zofiabaatar* the pterygoid fossa and pterygoideus shelf are especially large.

Simpson (1926, see also Fig. 13A in this paper) reconstructed the masticatory musculature of the allodontine *Ctenacodon*. M. masseter as reconstructed by Simpson has the topography as in modern therian mammals, e.g., *Didelphis*, *Canis* and *Equus* (Saban 1968; Turnbull 1970; Getty 1975; Evans & Christensen 1979). M. temporalis in Simpson's reconstruction does not reach the sagittal and lambdoidal crests (which is not possible since these crests form in the temporalis fascia), and its origin expands far anteriorly, m. pterygoideus does not reach the anterior margin of the pterygoid fossa. Simpson (1926: p. 236) stated that: 'There is no indication of separate insertions for two pterygoids', however, we believe that the clear division of the medial side of the posterior part of the dentary into pterygoid fossa and pterygoid fovea, observed by us not only in studied taeniolabidoid taxa, but also on the cast of the dentary of *Ctenacodon*, gives such an indication. Simpson reconstructed m. buccinator in place where we reconstruct masseter medialis pars anterior in *Nemegtbaatar*. We reconstruct the attachments of buccinator (Figs 6, 8), as it is placed in the majority of extant therians (but not in man) (Gambaryan 1989).

In Early Cretaceous plagaulacoid multituberculates from Mongolia the anterior zygomatic ridge is present in *Monobaatar*, where it is less prominent than in the studied Taeniolabidoidea (Kielan-Jaworowska *et al.* 1987: Pl. 3: 3). Partial lower jaw has been preserved only in *Eobaatar*, but the bone surface is poorly preserved and the muscular attachments cannot be recognized.

Ptilodontoidea. — Among the Ptilodontoidea the anterior zygomatic ridge has been preserved in *Prochetodon tardus* (Krause 1987: Fig. 4A) and in *Parectypodus clemensi* (Sloan 1981: Fig. 6.6A), but the drawing of the latter species does not show the details. The most complete ptilodontoid skulls belong to *Ptilodus montanus* USNM 6076 (Simpson 1937; Krause 1982; Wall & Krause 1992) and *Ectypodus tardus* PU 14724 (Sloan 1979). On the cast of this *Ptilodus* skull we recognize anterior and posterior zygomatic ridges, the intermediate one is poorly preserved. The identical position and shape of these two ridges in *Ptilodus* and in the Taeniolabidoidea allows us to suggest that in the Ptilodontoidea there were also three ridges on the zygomatic arch, as is characteristic of the Taeniolabidoidea. If so, in all the Cimolodonta, masseter superficialis consisted of two parts, as reconstructed in Figs 6 and 7 for the Taeniolabidoidea. In Fig. 4A we present the photograph of the dentary of *Ectypodus szalayi*, in which the masseteric fovea is confluent with the anterior part of the masseteric fossa, as described above for *Kryptobaatar*.

Sloan (1979; see also Fig. 13B in this paper) reconstructed the masticatory musculature of *Ectypodus tardus*. In his reconstruction masseter medialis pars anterior (referred to as the anterior deep masseter) is generally similarly placed as in our reconstructions of Asian taeniolabidoids (Figs 6, 7). In Sloan's reconstruction it originated from the orbital pocket as in multituberculates studied by us, but inserted a little more posteriorly. Masseter medialis pars anterior in extant mammals occurs in hystricomorph and myomorph rodents (Fig. 5), it is absent in sciuromorph rodents (Tullberg 1899; Saban 1968; Turnbull 1970). In the Bathyergidae it originates from the orbital pocket (Boller 1970), where there is also an orbital ridge, as in studied multituberculates. In rodents in which this muscle is present, the anterior edge of the zygomatic arch originates more anteriorly (opposite the premolars) than in sciuromorph rodents, where this muscle is lacking and the zygomatic arch originates to the rear of the molars. In cimolodont multituberculates the zygomatic arch originates far anteriorly, opposite p4, which is evidently related to the presence of masseter medialis pars anterior. According to our reconstructions (Figs 6, 7) this muscles inserted in a masseteric fovea (which is especially distinct in *Chulsanbaatar* Figs 2C, 12H, and in *Catopsbaatar* — not figured here). In hystricomorph and myomorph rodents masseter medialis pars anterior inserts in front of the basis of the coronoid process, in most studied multituberculates it inserted in front and ventral to the basis of the coronoid process, but within the anterior part of the masseteric fossa in *Kryptobaatar* and *Ectypodus* (Fig. 4). In these rodents masseter medialis pars anterior inserts on a large tubercle; in multituberculates its muscular part inserted in the fovea and the aponeurosis on the ridge around the fovea.

In Sloan's (1979: Fig. 3) reconstruction of the *Ectypodus* skull masseter superficialis has a topography as in extant myomorph rodents (Fig. 5, and e.g., Rinker 1954; Turnbull 1970) and differs from our reconstructions in Asian taeniolabidoids (Figs 6, 7). We base our reconstructions of this

muscle (divided into two parts) in the Taeniolabidoidea on the presence of distinct anterior and intermediate zygomatic ridges on the zygomatic arch (Fig. 2) for its origin. As argued above, such ridges possibly occurred in all the multituberculates and, if so, masseter superficialis in *Ectypodus* could not be directed anterodorsally — posteroventrally, as reconstructed by Sloan (1979: Fig. 3), and should rather consist of two parts, each directed perpendicular to the relevant zygomatic ridge.

Other multituberculates. — The two multituberculate families assigned to the suborders *incertae sedis*, the Cimolomyidae and Arginbaatariidae do not provide much information on the structures related to the muscular attachments. In the cimolomyid *Meniscoessus* the anterior zygomatic ridge has been preserved (Clemens 1973: Fig. 30d–e; see also Archibald 1982). In *Arginbaatar* the anterior zygomatic ridge is weak (Kielan-Jaworowska *et al.* 1987: Pl. 21: 2), and the partial lower jaws are badly damaged and do not show the muscle scars.

Functional analysis

We follow the division of Hiiemae & Ardran (1968) of the chewing cycle into preparatory stroke, power stroke and recovery stroke. This scheme has been subsequently replaced (e.g., Hiiemae 1978; Weijs 1994 and references therein) by a division into: closing (fast close), power (slow close) and opening stroke (divided into slow open and fast open). Dealing with fossil material, however, we were unable to recognize these phases, which may be studied only in extant mammals. Weijs & Dantuma (1975) recognized e.g., 16 phases in *Rattus*, which cannot be reconstructed in fossil forms. We do not discuss deglutition.

Hiiemae (1971) and many others, established the vectors using the centers of the areas of attachment and the same system is applied here (Fig. 8). The authors studying extant mammals evaluate the force of the muscles using the mass (weight or volume) or physiological section of the muscles, expressed as a percentage of the total weight of all the muscles (e.g., Schumacher & Rehmer 1962; Turnbull 1970; Hiiemae 1971, and others). As such methods are not possible in fossil material, we follow Crompton & Hotton (1967) in establishing the muscle forces using the size and prominence of the attachment areas and reconstructing the size of the muscles. The estimates based on the size and prominence of the attachments are of course highly subjective. However, as seen in Table 1, the obtained sizes of the vectors for multituberculates fall within the range of the vectors of extant rodents. For comparison we made estimates of the vectors for the following extant mammals: *Ellobius* (based on original material), and of *Hystrix, Sciurus, Rattus, Equus, Ovis* and *Odocoileus* (all based on data from Turnbull 1970), and in all cases we obtained the protractory horizontal component for the resultant force. The direction of the horizontal components of the resultant forces in multituberculates is
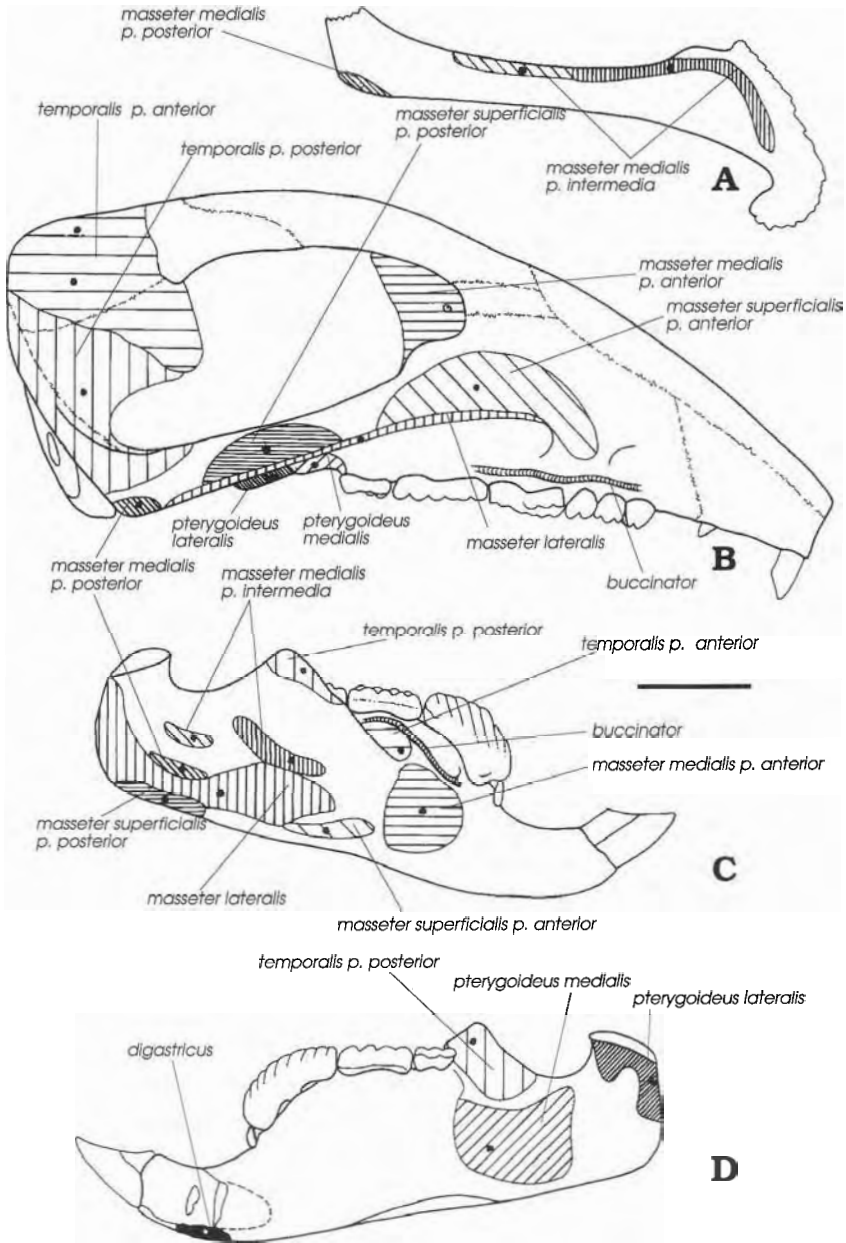
Fig. 8. Reconstruction of muscle attachments in *Nemegtbaatar* skull and lower jaw, based on the surface topography of the bones. A. Mirror image of the medial view of the right zygomatic arch. B. Lateral view of the skull. C. Lateral view of the lower jaw. D. Medial view of the lower jaw. Black points — centers of the attachments areas of the muscles. The upper and lower black points on the attachment area of temporalis p. anterior show the centers of temporalis p. superficialis and temporalis p. anterior respectively (see Fig. 6). The muscle referred to as digastricus may be detrahens mandibulae as in monotremes. Masseter lateralis profundus is referred to as masseter lateralis. Scale bar — 5 mm.

Table 1. Vectors of force of masticatory muscles in percent of the algebraic sum of vectors of all the muscles.

Muscles	Genera					
	Neme	Cato	Ello	Hyst	Sciu	Ratt
Masseter superficialis p. anterior	15.4	16.1	15.2	31.3	19.1	18.8
Masseter superficialis p. posterior	7.7	9.7				
Masseter lateralis profundus	15.4	16.1	25.3	12.9	31.0	22.1
Masseter medialis p. anterior	11.5	12.9	5.1	16.3	–	6.6
Masseter medialis p. intermedia 1	5.8	4.8	3.8	11.3	10.9	6.6
Masseter medialis p. intermedia 2	3.8	3.2				
Masseter medialis p. posterior	3.8	3.2	2.5			
Temporalis superficialis	3.8	3.2	2.5	16.6	19.4	32.6
Temporalis p. anterior	7.7	6.4	17.7			
Temporalis p. posterior	7.7	6.5	17.7			
Pterygoideus lateralis	5.8	4.8	3.8	6.0	7.3	4.4
Pterygoideus medialis	11.5	12.9	6.3	5.5	12.3	8.8

Estimates of vectors of *Nemegtbaatar* and *Catopsbaatar* are approximate, based on the size and prominence of the attachment areas.
Neme — Nemegtbaatar; Cato — Catopsbaatar; Ello — Ellobius; Hyst — Hystrix*; Sciu — Sciurus*; Ratt — Rattus*. Numbers 1 and 2 of the *masseter medialis p. intermedia* correspond to the anterior and posterior bellies of this muscle, respectively.
* After Turnbull (1970).

retractory and in the extant herbivorous mammals it is protractory. This dramatic difference depends mostly on the topography of the muscles, rather than on their size. The relation of the vertical and horizontal components of the vectors of particular muscles and the size of their moment arms depend only on the topography of the muscles and not on the size.

We use the following signs for the direction of the lines of muscle action, expressed in components along different movements: positive numbers for the backward (retractory movement); negative numbers (-) for the forward (protractory movement); positive numbers for the elevation (closing movement); negative numbers (-) for the depression (opening movement). Fig. 10 shows the vectors of all the masticatory muscles at the power stroke in *Nemegtbaatar*. Similar drawings were made for all the stages of *Nemegtbaatar* in Fig. 9, but are not presented here; force components and moments of the masticatory muscles obtained from these drawings are given in Table 2. Drawings, as in Fig. 10, were also made for *Catopsbaatar*, and the relevant data are given in Table 3.

Recovery and preparatory strokes (Fig. 9B, C). — In extant mammals (e.g., *Rattus*; see Weijs 1975; Weijs & Dantuma 1975) at the beginning of the recovery stroke, the lower jaw is in a protracted position; it proceeds forward at early opening and subsequently moves backwards. In multituberculates, in contrast, at the beginning of the recovery stroke the lower jaw was in a retracted position, and the resultant force of all the muscles had a very small retractory horizontal vector component (Fig. 9A). At this
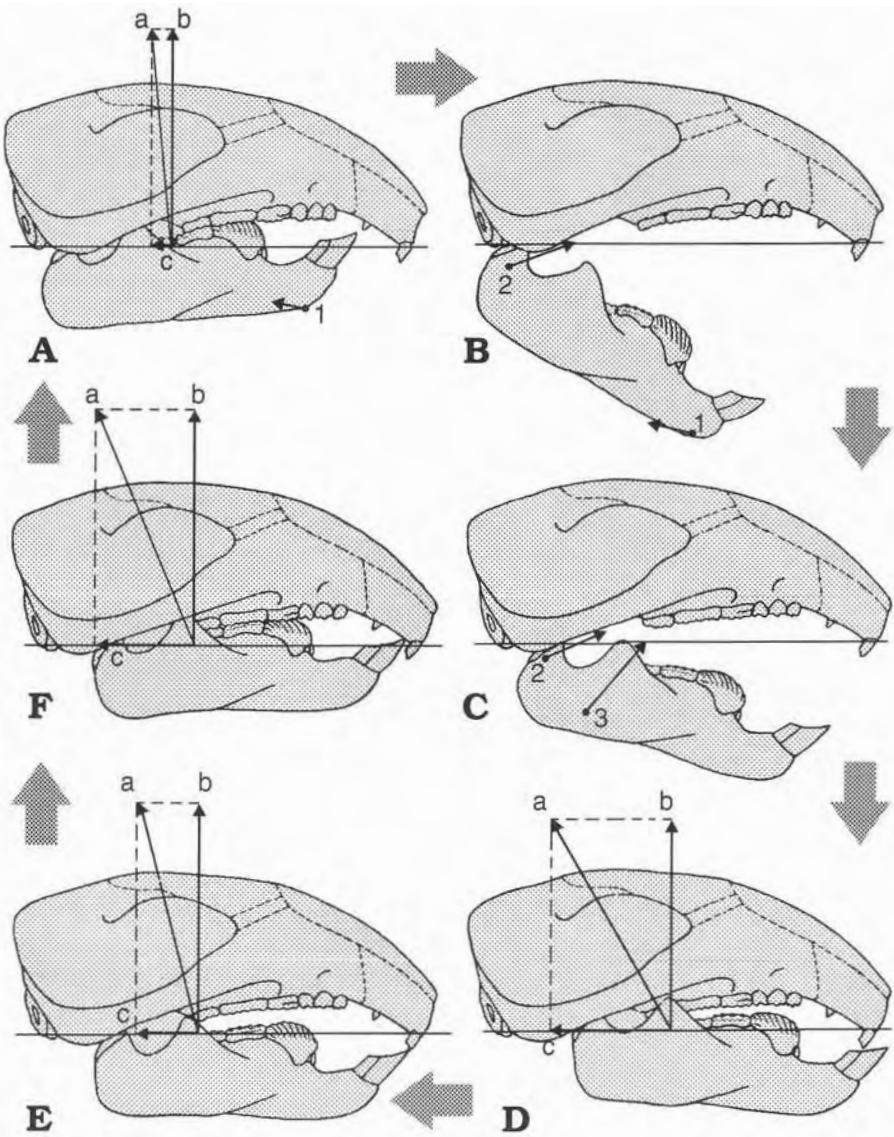
Fig. 9. Reconstruction of the masticatory cycle in *Nemegtbaatar*. A. End of the power stroke and beginning of the recovery stroke. B, C. Recovery and preparatory strokes. D, E. Beginning and end of the incisive action. F. Beginning of the power stroke. The bold arrows (a, b, c) denote resultant forces and their components of all the masticatory muscles: a — resultant force; b — vertical component; c — horizontal component; 1, 2, 3 — vectors of: digastricus, pterygoideus lateralis and masseter lateralis profundus respectively; black points at the beginning of the vectors — centers of the attachments areas of the muscles.

moment all the masticatory muscles relaxed and the recovery stroke began, as in extant mammals, by the action of m. digastricus, which initiated the opening of the mouth (Fig. 9B).

Table 2. Force components and moments of the masticatory muscles in *Nemegtbaatar.*

Muscles	Incisive action				Power stroke					
	start		end		start		middle		end	
	A	B	A	B	A	B	A	B	A	B
Masseter superficialis p. anterior	42	28	11	38	22	40	8	43	6	42
Masseter superficialis p. posterior	95	-7	39	5	56	4	41	10	20	12
Masseter lateralis profundus	-6	17	-47	23	-33	24	-53	25	-68	25
Masseter medialis p. anterior	55	35	24	45	37	45	24	49	13	50
Masseter medialis p. intermedia 1	47	18	11	28	14	28	-1	31	-21	30
Masseter medialis p. intermedia 2	144	1	66	10	83	9	45	10	24	16
Masseter medialis p. posterior	254	-15	110	-9	151	-9	110	-5	73	-6
Temporalis p. anterior	171	14	130	21	144	22	139	26	126	26
Temporalis p. posterior	576	4	283	9	390	9	272	11	248	11
Pterygoideus lateralis	-85	2	-146	4	-135	4	-154	4	-167	5
Pterygoideus medialis	143	1	26	22	46	21	18	28	-1	29
Resultant forces	60	20	25	26	40	26	23	31	10	32

A. Horizontal component of the force vector in percent of the vertical component.
B. Muscle moment arm length in percent of the jaw length.
Numbers 1 and 2 of the *masseter medialis p. intermedia* correspond to the anterior and posterior bellies of this muscle, respectively.
Minus in A is used for the protractory components, in B for the moment arm of the depression. Positive numbers in A are used for the retractory components, in B if the muscle produces a jaw elevating moment.

In multituberculates, at the beginning of the recovery stroke four parts of the masticatory muscles had protractory horizontal vector components (Tables 2, 3). Masseter lateralis profundus and pterygoideus lateralis had the greatest components: (-68) and (-165) in *Nemegtbaatar*, and (-117) and (-79) in *Catopsbaatar*, respectively. It seems that when the mouth was already open (because of the action of m. digastricus — Fig. 9B), only m. pterygoideus lateralis initiated anterior movement of the lower jaw. Masseter lateralis profundus at this point could not work, as it is one of the most powerful muscles, having a great moment (25% of the length of the lower jaw in *Nemegtbaatar* and 27% in *Catopsbaatar*, that of pterygoideus lateralis is 5% of the length of the lower jaw in both taxa). If masseter lateralis profundus would work at the beginning of this stage, the mouth would close and the forward movement of the lower jaw would be impossible. In addition, when the mouth opened (Fig. 11), at the largest gape the moment of masseter lateralis profundus decreased 1.3 times, that of pterygoideus lateralis (not shown in Fig. 11 because of small size) decreased reaching zero. Therefore at this stage only the horizontal vector component of m. pterygoideus lateralis was left.

During the preparatory stroke that followed (Fig. 9C), the lower jaw moved upwards and the mouth closed. As shown by Hiiemae & Ardran (1968), Crompton & Hylander (1986), Weijs & Dantuma (1975), and

Table 3. Force components and moments of the masticatory muscles in *Catopsbaatar*.

Muscles	Incisive action				Power stroke			
	start		end		start		end	
	A	B	A	B	A	B	A	B
Masseter superficialis p. anterior	24	31	5	37	3	39	-13	40
Masseter superficialis p. posterior	113	7	79	12	79	14	63	17
Masseter lateralis profundus	-26	27	-61	29	-78	29	-117	27
Masseter medialis p. anterior	47	37	26	43	31	45	17	46
Masseter medialis p. intermedia 1	46	26	18	31	12	33	-9	34
Masseter medialis p. intermedia 2	58	15	26	20	18	22	0	23
Masseter medialis p. posterior	142	-7	99	-4	97	-3	77	-3
Temporalis superficialis	116	19	95	22	87	23	73	24
Temporalis p. anterior	163	14	129	18	119	18	106	19
Temporalis p. posterior	248	14	220	16	214	17	175	17
Pterygoideus lateralis	-18	-2	-30	2	-49	4	-79	5
Pterygoideus medialis	138	0	89	5	93	7	70	10
Resultant forces	55	22	35	25	30	29	16	30

A. Horizontal component in percent of the vertical component.
B. Muscle moment arm length in percent of the jaw length.
Numbers 1 and 2 of *masseter medialis p. intermedia* correspond to the anterior and posterior bellies of this muscle, respectively.
Minus in A is used for the protracotory components, in B for the moment arm of the depression. Positive numbers in A are used for the retractory components, in B for the moment arm of the elevation.

others, during the beginning of the preparatory stroke in extant mammals only some muscles are involved. In multituberculates two strong muscles (masseter superficialis pars anterior and masseter lateralis) and two weak muscles (masseter medialis pars intermedia and pterygoideus lateralis) that had high protractory horizontal vector components initiated the preparatory stroke (Tables 2, 3). At the end of the preparatory stroke only the vectors of masseter lateralis and pterygoideus lateralis had protractory horizontal components (Fig. 9D), the lower jaw moved upwards, and all the muscles that worked during the incisive action and had now retractory vector horizontal components (two parts of masseter superficialis, four parts of masseter medialis, three parts of m. temporalis and m. pterygoideus medialis) began their action.

Incisive action (biting) (Fig. 9D, E). — The incisive action in rodents is normally repeated several times, and the same was possibly the case in taeniolabidoid multituberculates. We do not discuss here the repetition of the incisive action. During the incisive action only two muscles showed a protractory horizontal vector component: masseter lateralis profundus and pterygoideus lateralis (Tables 2, 3). It is possible that at the end of the preparatory stroke pterygoideus lateralis relaxed. Masseter lateralis profundus, although having a protractory horizontal vector component, poss-
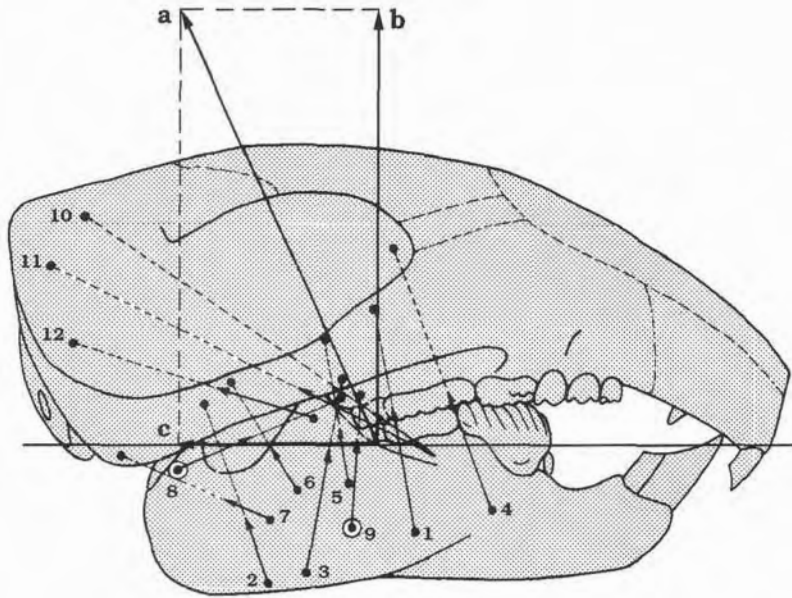
Fig. 10. Resultant force and its components in *Nemegtbaatar* at the power stroke. a — resultant force; b — vertical component; c — horizontal component; 1–12 vectors of: 1, 2 — masseter superficialis p. anterior, p. posterior; 3 — masseter lateralis profundus; 4, 5, 6, 7 — masseter medialis p. anterior, p. intermedia anterior belly, p. intermedia posterior belly, p. posterior; 8 — pterygoideus lateralis; 9 — pterygoideus medialis; 10, 11, 12 — temporalis p. superficialis, p. anterior, p. posterior. The scale of the resultant force and its components is twice smaller than the scale of the individual vectors. Black points — centers of the attachments areas of the muscles; black circles with points — centers of the attachments areas of the muscles, inserting on the medial side of the lower jaw.

ibly still continued its action during the biting. It is one of the largest muscles, with a large moment arm, and its protractory horizontal vector component had a bearing on the more anterior position of the resultant forces. This in turn increased the moment arm of the resultant forces. The protractory horizontal vector component of masseter lateralis profundus increased during the work of the incisors, from -6 to -47 in *Nemegtbaatar* and from -12 to -43 in *Catopsbaatar*. The force of the retractory horizontal vector components of all other muscles was so great that, in spite of the protractory horizontal component of the vector of masseter lateralis profundus, the jaw moved posteriorly. However, the protractory horizontal vector component of some muscles was advantageous at this stage, as it increased the moment arm of the resultant force of all the muscles.

At the beginning of the power phase of the incisive action the upper and lower incisors (Fig. 9D) came into contact and the lower incisor contacted the upper one with its posterior tip; the contact prolonged during the backward movement of the lower jaw, as long as the anterior tips of the upper and lower incisors contacted one another (Fig. 9E). A sharp anterior point and a beveled facet on the upper incisor, and a sharp anterior point
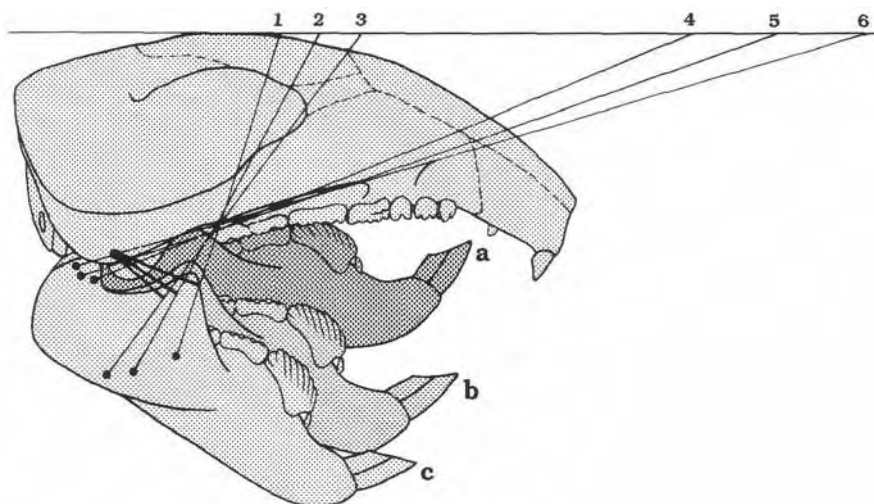
Fig. 11. Changes of the moments (bold lines) and the direction of the vectors of masseter lateralis profundus (1, 2, 3) and of the direction of vectors of pterygoideus lateralis (4, 5, 6) during the gape in *Nemegtbaatar*. 1, 4, a — the beginning of the gaping, 2, 5, b — middle of the gaping, 3, 6, c — end of the gaping; black points — centers of the attachments areas of the muscles.

and a concave facet on the lower incisor, were produced during this action due to the structure of the self-sharpening incisors (with limited enamel band). The great retractory horizontal vector component of most of the masticatory muscles allowed the lower incisor to move posteriorly, even though in doing so, it had to overcome the vertical stress of the ventrally concave upper incisor. Because of this the cutting force of the incisors was very strong.

Power stroke (Figs 9F, A; 10). — When the work of the incisors was finished, the grinding action of the premolars and molars started. Changeover from the work of the incisors to that of the premolars and molars was associated with the increase of the retractory horizontal component of the vectors of the following parts of masseter: masseter superficialis pars anterior and pars posterior, masseter medialis pars anterior and pars intermedia. This increase was greater in *Nemegtbaatar* than in *Catopsbaatar* (Tables 2, 3). In *Catopsbaatar* at the end of the power stroke, the protractory horizontal vector component occurred in the work of masseter superficialis pars anterior. In *Nemegtbaatar* this muscle had a retractory horizontal vector component until the end of the power stroke. In *Catopsbaatar* the vector of masseter superficialis pars posterior had a greater retractory horizontal component (63% of the vertical component) than in *Nemegtbaatar* (20%) and as a result, m. superficialis pars anterior and pars posterior had a similar joint retractory horizontal vector component in both taxa. In extant therians masseter superficialis works as the main protractor of the lower jaw (Turnbull

1970; Hiiemae & Ardran 1968; Weijs & Dantuma 1975, and others). The retractory horizontal vector component of masseter superficialis in multituberculates is unique for mammals.

Comparisons. — In rodents and in small herbivorous marsupials m. masseter inserts more anteriorly on the lower jaw than in other therian mammals, e.g., in carnivores, insectivores, large herbivores, primates, etc. (Table 4 and Fig. 12). In multituberculates masseter inserted still more anteriorly than in rodents and in small herbivorous marsupials, which was especially strongly expressed in small forms such as e.g., *Chulsanbaatar.* Anterior insertion of the masseter muscles in multituberculates resulted in a more anterior position of the masseteric crest and masseteric fossa than in therians. The masseteric fovea, characteristic of multituberculates is also placed far anteriorly. It does not occur in therian mammals, but its anterior margin corresponds to the anterior margin of the masseter insertion in other mammals. Not only masseter but also m. temporalis pars anterior inserted in multituberculates more anteriorly than in therian mammals, in relation to which the coronoid process in multituberculates is placed more anteriorly than in therians (Table 4).

Multituberculates differ from therians among others in the more posterior position of the postorbital process and parietal crest (temporal line). This was related to the more backward origin of m. temporalis than in therians. In studied multituberculates all parts of m. temporalis were directed posterodorsally — anteroventrally (Figs 6, 7), while in therians the anterior and superficial parts of m. temporalis, usually are directed vertically, and sometimes even anterodorsally — posteroventrally (Fig. 5). Anterior insertion of the masticatory muscles in multituberculates was related to the backward chewing stroke: it resulted in an increase of the moment arm and in the retractory horizontal component of the resultant force of all the masticatory muscles.

Bramble (1978) proposed the bifurcal model of the work of masticatory apparatus, in which (p. 171) "the bite point may be regarded as a distinct and independent 'occlusal fulcrum' equal in status to the jaw articulation or 'joint fulcrum' ". Using Bramble's model we argue that in therians, in which the resultant force of all the masticatory muscles is inclined forwards (has a protractory horizontal component), insertion of the masseter on the lower jaw cannot be placed far anteriorly, as the force generated at the condylar process will be directed downwards and the dislocation at the temporomandibular joint will occur. As in multituberculates the resultant force of all the muscles, in contrast, was inclined backwards (had the retractory horizontal component), the anterior insertion of masticatory muscles occurred (Table 4).

In extant herbivorous mammals, the ventral surface of the upper premolars and molars (in lateral view) is either horizontal (e.g., Macropodidae, Equidae, and most Rodentia), or convex (Artiodactyla and some Rodentia). In multituberculates this surface is slightly arcuate (concave) with M1 in the middle (see e.g., Fig. 2 in this paper and the photographs
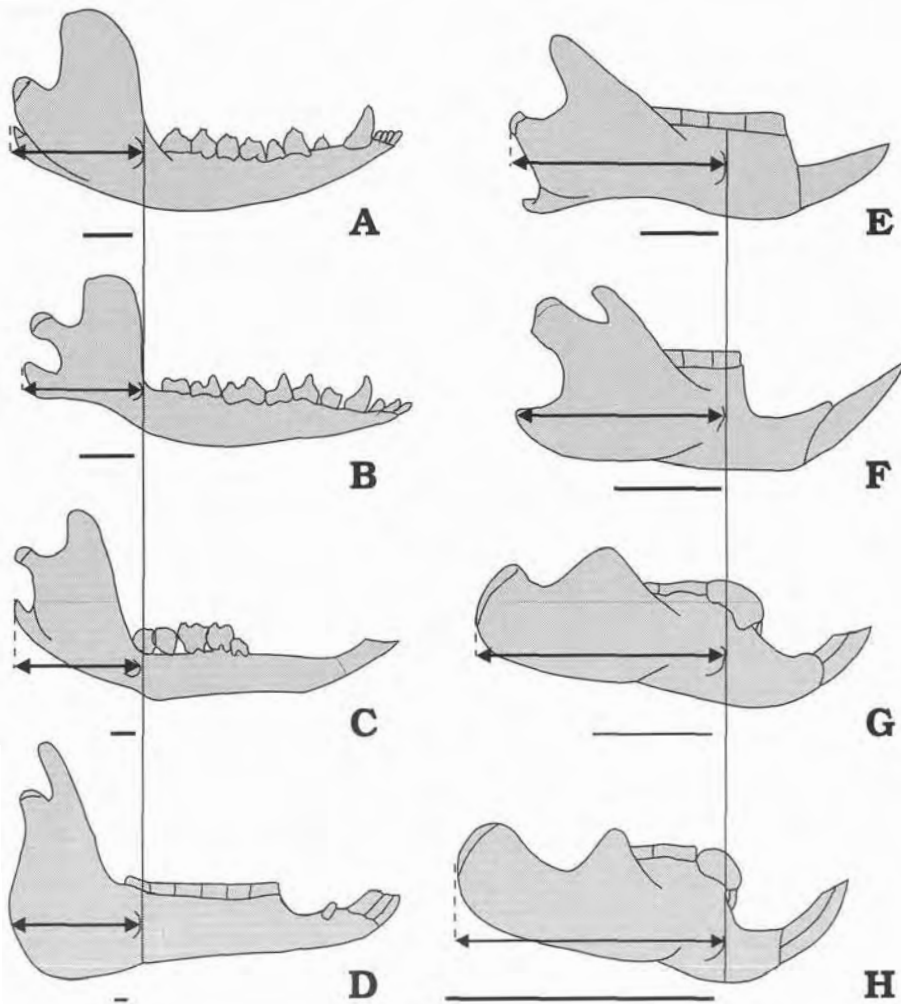
Fig. 12. Comparison of lower jaws in lateral view, rendered to the same length. □A. *Didelphis* (omnivore-carnivore). □B. *Echinosorex* (insectivore). □C, D. *Macropus, Equus* (large herbivores). □E. *Dactylopsila* (small herbivorous marsupial). □F. *Rattus* (rodent). □G, H. *Nemegtbaatar, Chulsanbaatar* (multituberculates). Vertical lines — anterior margin of masseter; arrows — distance between anterior margin of masseter and end of the jaw. Scale bars — 10 mm.

in Broom 1914; Kielan-Jaworowska 1970, 1971, 1974; Miao 1988). Such structure of P4 — M2 row increased the stress during the grinding (as in the case of the incisors). During the backward movement of the lower jaw the p4 in *Nemegtbaatar* and *Catopsbaatar* (as calculated from the length of the glenoid fossa) reached the anterior margin of the inner cusp ridge of M1 and was stopped by it. In multituberculates, as in therian mammals (Schaller 1992) there would have been a disc in the temporomandibular joint, dividing it into two chambers. As demonstrated by Weijs (1975) and Zubtsova (1986, 1990), because of the work of the disc in rodents, the

Table 4. Relative dimensions of the morphological elements of the lower jaw as percent of total length (see Figs 1 and 12).

Genera	A	B	C	D	E	F	G
Nemegtbaatar	67	51	14	39	56	5	8
Kryptobaatar	62	53	11	44	56	6	11
Chulsanbaatar	76	53	14	47	58	8	11
Sloanbaatar	67	52	12	48	55	5	10
Catopsbaatar	69	48	21	39	54	4	1
Rattus	54	42	20	38			
Sciurus	51	42	36	21			
Hystrix	50	36	9	16			
Didelphis	39	38	19	23			
Macropus	32	32	17	29			
Bettongia	48	45	19	27			
Dactylopsila	56	53	20	34			
Equus	32	23	17	14			
Capra	32	31	17	12			

A. Distance between the posterior margin of the jaw and the anterior margin of the masseteric fovea (in therians: anterior margin of the insertion of the masticatory muscles).
B. Distance between the posterior margin of the jaw and the anterior margin of the coronoid process.
C. Height of the coronoid process.
D. Distance between the posterior margin of the jaw and the anterior margin of the pterygoid fossa.
E. Distance between the posterior margin of the jaw and the anterior margin of the masseteric crest.
F. Width of the masseteric crest.
G. Width of the pterygoideus shelf.
The characters in columns E, F, and G are given only for multituberculates, because the masseteric crest in multituberculates is not homologous to that in therians, and the pterygoideus shelf does not occur in therians.

range of the translation in this joint increases. In the Dipodidae the articulation surface of the condylar process extends anteriorly beyond the glenoid fossa, articulating with the disc. In multituberculates in the backward position of the lower jaw the condylar process could not extend beyond the glenoid fossa, the posterior margin of which is confluent with the posterior margin of the zygomatic arch. In the most forward position, the disc may be supported by the zygomatic arch and the condylar process apparently could reach a position in front of the glenoid fossa.

Krause (1982) agreed with Clemens (1963: p. 72) that the elongate, slender structure of ptilodontoid incisors suggests 'a mechanism for grasping, holding and piercing'. In Krause's (1982: Figs 6, 11) reconstruction of the *Ptilodus* skull, however, the contact of the upper and lower incisors is not evident. We speculate that the lower incisors in *Ptilodus* could contact the upper ones because of the action of the disc. In addition, in many reconstructions of multituberculate skulls in the lateral view (e.g.,
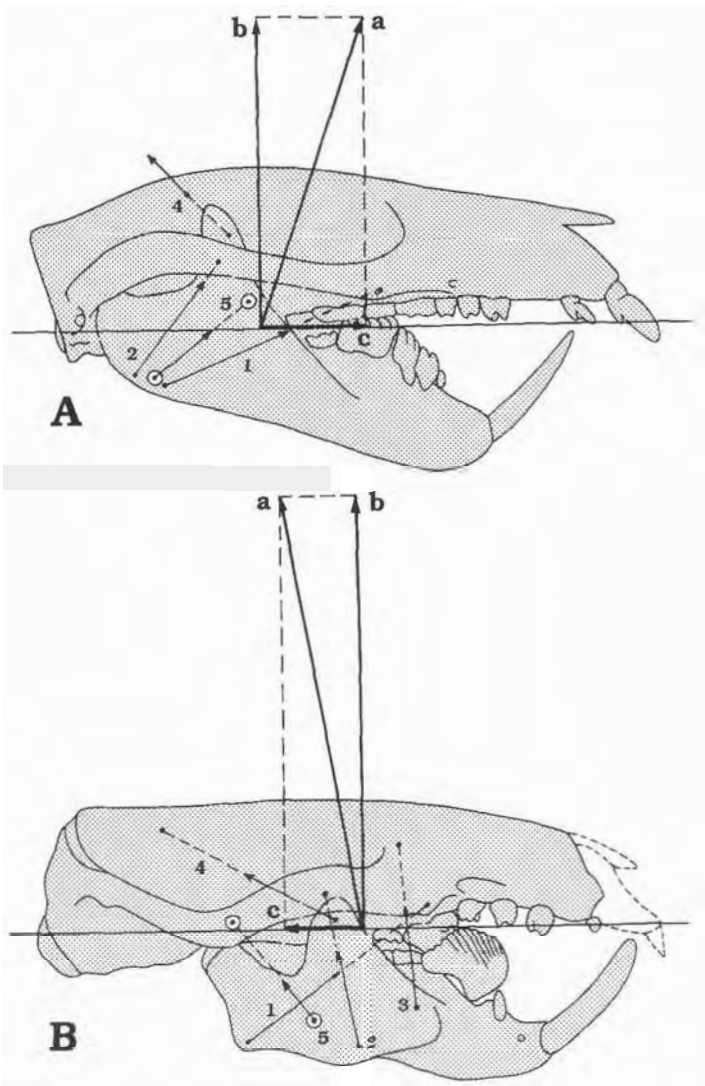
Fig. 13. Restorations of the masticatory muscles. □A. *Ctenacodon serratus* (after Simpson 1926). □B. *Ectypodus tardus* (after Sloan 1979), modified by vectors added and reversed, not to scale. 1–5 — vectors of masseter superficialis, masseter lateralis profundus, masseter medialis p. anterior, temporalis and pterygoideus, respectively; a — resultant force; b — vertical component; c — horizontal component; black points — centers of the attachments areas of the muscles; black circles with points — centers of the attachments area of the muscles, inserting on the medial side of the lower jaw. Note the protractory resultant force in *Ctenacodon* (as in Theria) and retractory in *Ectypodus* (as in other multituberculates). Sloan's reconstruction of *Ectypodus* skull (not emended here) resembles that of therians rather than multituberculates in having the braincase elongated posteriorly behind the glenoid fossa and the angular process (absent in multituberculates).

Simpson 1937; Kielan-Jaworowska *et al.* 1986; Krause 1982; Wall & Krause 1992) the snout is completely straight rather than bent ventrally.

The ventral slope of the snout is seen in all well-preserved skulls in the studied material (see e.g., Fig. 2 in this paper, and photographs in Kielan-Jaworowska 1970, 1971, 1974, and Kielan-Jaworowska *et al.* 1986). If the anterior part of the skull in *Ptilodus* were reconstructed with a similar ventral bend, the contact of the upper and lower incisors would be better.

Previous reconstructions. — In order to test the earlier reconstructions of multituberculate musculature, namely of *Ctenacodon* by Simpson (1926) and of *Ectypodus* by Sloan (1979), we modified their drawings with vectors of all the muscles added (Fig. 13). The resultant force in *Ctenacodon* gave a large protractory horizontal component, as characteristic of therians, but not of the multituberculates. This shows that the reconstruction of the musculature of *Ctenacodon* is incorrect. In the case of *Ectypodus* we obtained the retractory horizontal component for this force, as in taeniolabidoid multituberculates (this paper) and in *Ptilodus* (Wall & Krause 1992).

The reconstruction of vectors by Wall & Krause (1992) for *Ptilodus* differs from our reconstructions of the Taeniolabidoidea mostly in a different position of the vector of m. temporalis pars anterior (anterior temporalis of Wall & Krause), which in their reconstruction has a protractory horizontal component, and in our reconstructions it has a retractory horizontal component. In extant mammals with a postorbital process, the origin of m. temporalis never extends in front of this process. The reconstruction of this muscle in *Ptilodus* thus depends on the position of the postorbital process. If the postorbital process was indeed situated in this taxon on the frontal (Simpson 1937: Figs 4, 5) as in most therian mammals, then the eye in *Ptilodus* would be unusually small and the reconstruction of m. temporalis by Wall & Krause may be correct (see discussion on pp. 82 and 83). If, however, the postorbital process was situated in *Ptilodus* as in Asian Cretaceous taeniolabidoids on the parietal, the area shown by Wall & Krause (1992: Fig. 2) as the origin of m. temporalis anterior, would more likely correspond to the origin of the dorsal part of the orbital ligament (see e.g., Evans & Christensen 1979). Even if m. temporalis pars anterior would originate as reconstructed by Wall & Krause (1992), it inserted anteroventrally to the coronoid process, as reconstructed by us for *Nemegtbaatar* (Figs 6D, 8) and therefore its vector could not have a protractory horizontal component. M. pterygoideus medialis (internal pterygoid of Wall & Krause 1992) in their reconstruction is directed almost vertically, we believe that it should be arranged more horizontally, being inserted more anteriorly, as reconstructed by Sloan (1979) and by us (Figs 8D, 10).

Gingerich (1984) stated that the motion of the lower jaw in multituberculates was powered largely by the temporalis complex rather than by the masseter-pterygoid complex. Our studies do not confirm this conclusion. Even in the Plagiaulacoidea, which have a very large coronoid process and strong biting incisors, the masseter was a powerful muscle. As may be

seen from the above analysis and comparisons, the characteristic feature of the taeniolabidoid masticatory apparatus is the development of the complicated masseter-pterygoideus complex, expressed by the presence of strong zygomatic ridges, a prominent masseteric crest and a wide ptery-goideus shelf. As discussed above these features occur in all the multi-tuberculates. The taeniolabidoid taxa studied here differ in details of the relative sizes of the particular muscles and their positions. Taeniolabididae apparently had stronger m. temporalis than the Eucosmodontidae, in which the coronoid process is very low. In spite of differences, the general pattern of the arrangement of the masticatory muscles was similar not only in all the Cimolodonta, but possibly in all the multituberculates.

Anatomical implications

Position of jugal. — Hopson *et al.* (1989) described the multitubercu-late jugal that, unlike in other mammals, lies against the medial surface of the zygoma and was not exposed laterally. They suggested (Hopson *et al.* 1989: p. 201) that 'the expansion of the zygomatic process of the maxilla and restriction of the jugal to the inside of the zygoma, where it spans the maxillary-squamosal suture, served to increase the ability of the zygoma to resist primarily downward bending and longitudinal compression caused by forces exerted by enlarged masseter muscles in the earliest multituberculates.' Reconstructions of masseter superficialis in Taenio-labidoidea (Figs 6, 7) allow us to speculate that in the evolution of multituberculates, the areas of origin of masseter superficialis pars anter-ior and pars posterior on the lateral surface of the zygomatic arch in-creased, pars anterior extending posteriorly and pars posterior anteriorly. An increase of the attachment areas of these muscles, presumably origin-ally placed at the zygomatic processes of the maxilla and squamosal, resulted in an increase of the size of these processes. The processes finally came into contact with one another, resulting in a migration of the jugal to the medial side of the zygomatic arch.

Postorbital process. — The oldest multituberculate skulls in which the postorbital process has been preserved are from the Late Cretaceous of Asia and belong to the Eucosmodontidae, Taeniolabididae and Sloan-baataridae. In Asian members of these families most of the cranial roof is built of the extensive frontals. The frontoparietal suture forms a wide arch that is convex posteriorly and there is no trace of the postorbital process on the frontals. The parietals form the whole cranial roof posteriorly and bear a prominent process at the end of the supraorbital crest, identified by Kielan-Jaworowska (1970, 1971, 1974), Clemens & Kielan-Jaworowska (1979), and Kielan-Jaworowska *et al.* (1986) as the postorbital process. Miao (1993: p. 69) incorrectly indicated that according to Kielan-Jaworow-ska *et al.* (1986) the postorbital process is absent in multituberculates, and regarded its absence as one of the multituberculate apomorphies.

In advanced Paleocene Taeniolabididae, of which the skulls have been preserved, namely in the North American *Taeniolabis* (Broom 1914; Granger & Simpson 1929; Simpson 1937; Sloan 1981) and in the Asian *Lambdopsalis* (Miao 1988), the frontals are relatively small and pointed posteriorly. There is a prominent sagittal crest (absent or very small in Asian Cretaceous taxa) and the parietals slope ventrolaterally from it forming extensive concave areas for accommodation of the temporal muscles. One can visualize that, in relation to the increase of the cutting function of the incisors in the evolution of the Taeniolabididae, the size of m. temporalis increased, causing the forward migration of the postorbital process. The frontals in *Taeniolabis* and *Lambdopsalis* are pointed posteriorly and are smaller than in Asian Late Cretaceous genera.

The postorbital process of *Taeniolabis* has not been described, but as it may be inferred from the photographs and drawing published by Broom (1914), it was small and situated at the anterior part of the parietal. The reconstruction of the *Taeniolabis* skull by Granger & Simpson (1929), reproduced subsequently by Simpson (1937) and many others, was emended by Sloan (1981: Fig. 6.14). In Sloan's reconstruction the eye is larger, the orbital diameter calculated by him being about 35 mm. The postorbital process is situated in Sloan's reconstruction more anteriorly than in Asian skulls studied by us, but it is evidently placed on the parietal, which in *Taeniolabis* migrated forward shutting off the frontal from the rim of the orbit. The cranial roof in *Lambdopsalis* is similar to that of *Taeniolabis*, but Miao (1988) described the postorbital process in *Lambdopsalis* on the frontal, covered dorsally in part by the parietal. However, Jin Meng (personal communication, February 1995) informed us that in *Lambdopsalis* specimens studied by him, the postorbital process is on the parietal.

The position of the postorbital process in the Plagiaulacoidea and Ptilodontoidea is not known. Clemens & Kielan-Jaworowska (1979: Fig. 6–5D) presented a 'largely hypothetical restoration of a paulchoffatiid skull' with the postorbital process placed far anteriorly, in a similar position as reconstructed earlier by Simpson (1937) for *Ptilodus*. In the new reconstruction of the paulchoffatiid (*Pseudobolodon*) skull (Hahn & Hahn 1994: Fig. 2) the postorbital process has not been shown.

Simpson (1937: Figs 4, 5) reconstructed but did not describe the small postorbital process in *Ptilodus*, situated on the frontal as in most therians. It should be remembered, however, that Simpson described the *Ptilodus* skull on essentially therian lines. Krause (1982) modified slightly the reconstruction of Simpson, but not in respect to the position of the postorbital process. The only other fairly complete ptilodontoid skull is that of *Ectypodus* (PU 14724), the photograph of which was not published, but which was reconstructed by Sloan (1979: Fig. 2) with a small postorbital process on the frontal. In the same paper, the original drawing of the *Ectypodus* specimen (Sloan 1979: Fig. 1) does not show the postorbital process, but in the reconstruction of *Ectypodus* musculature (Sloan: Fig.

3) the eye is placed opposite, rather than in front of the reconstructed postorbital process. Krause (1986) measured the orbits in *Ptilodus* and *Ectypodus* on apparently inaccurate reconstructions of Simpson (1937) and Sloan (1979), and concluded that in these ptilodontoids the eyes were very small. The frontals in *Ptilodus* are pointed posteriorly, but in contrast to *Taeniolabis* are not excluded from the orbital rim. If large frontals with a rounded posterior margin are primitive for multituberculates, one can visualize that with an increase of the size of the temporal muscles in Ptilodontoidea, the sagittal crest appeared and the parietals moved laterally forward causing the change of the shape of the frontals. These changes occurred in parallel in the Taeniolabidoidea and in the Ptilodontoidea. In both suborders they were related to an increase of the work of the incisors, which, however, had different functions.

In most therian mammals, the postorbital process is situated on the frontal, but in e.g., *Procavia* and *Castor* (Grassé & Dekeyser 1955; Starck 1967), the postorbital process is situated either on the parietal, or at the boundary between the frontal and parietal (individual variation). In both these genera the parietals extend far anteriorly and embrace laterally the frontals. Because of the relatively enormous parietals in *Castor*, in spite of the parietal postorbital process, the eye is relatively small.

The parietal postorbital process in multituberculates is known only in the Taeniolabidoidea. It cannot be unequivocally demonstrated that the process primitively was situated in multituberculates on the parietal, although such a possibility appears probable. The posterior position of the postorbital process in Asian multituberculates implies the presence of very big eyes (Fig. 19), as characteristic of many extant nocturnal mammals, for example, *Allactaga*, *Meriones*, *Dipus* and many others (Nowak & Paradiso 1983).

Reconstruction of the multituberculate masticatory musculature presented above (Figs 6, 7), shows that the postorbital process on the parietal in studied Asian multituberculates functionally corresponds to the postorbital process situated on the frontal in most therians. The posterior position of the postorbital process in Asian multituberculates resulted in an oblique posterodorsal — anteroventral position of all the temporal muscles, different from those in therian mammals (see Fig. 5 and p. 76).

Glenoid fossa. — The multituberculate glenoid fossa (e.g., Miao 1993: Fig. 6.2) differs from that in therians in being relatively very large and being placed well lateral of the braincase. It is attached by a constricted pedicle, rather than placed very close to the braincase and anterolateral to the petrosal as in therians and monotremes. The longer axis of the multituberculate glenoid is directed anterolateral (more longitudinally than transversely), it is arranged transversely in most therians (but not in rodents), in monotremes, *Morganucodon* (Kermack *et al.* 1981) and *Sinoconodon* (Crompton & Luo 1993), or subtransversely in *Vincelestes* (Bonaparte & Rougier 1987). The multituberculate glenoid is flat, rather than

concave as in most therians, it slopes down and backwards and lacks the postglenoid process.

In Paulchoffatiidae (Hahn 1988: Pl. 11), the glenoid fossa is large and similar to that in cimolodonts, differing from the latter in being placed more posteriorly and having a less distinct pedicle. In *Lambdopsalis*, which is highly specialized, only the posterior part of the glenoid fossa has been preserved (Miao 1988). This fossa is set apart from the braincase, but there is no distinct pedicle, because of the expanded vestibular apparatus. The glenoid fossa is large and set apart from the braincase in docodonts (*Haldanodon*) as well, but it has no pedicle, is gently concave, has a more elevated posterior margin, and although it is arranged obliquely anterolaterally, its longitudinal axis is more transversely directed than in multituberculates (Lillegraven & Krusat 1991). An important difference is the bony external auditory meatus to the rear of the glenoid fossa in docodonts, which is absent in multituberculates. A glenoid fossa set apart from the braincase is a plesiomorphic feature for mammals, as the lower jaw joint in advanced cynodonts and tritylodontids (Kühne 1956; Barghusen 1968; Crompton & Hylander 1986), and the glenoid fossa in early mammals such as *Morganucodon*, *Sinoconodon*, *Haldanodon*, *Vincelestes* (Kermack *et al.* 1981; Crompton & Luo 1993; Crompton & Hylander 1986; Bonaparte & Rougier 1987) have such a position. In multituberculates, however, the glenoid fossa is derived, as it is positioned much further apart from the braincase than in the above cited mammals. This is because of the increase of the masticatory musculature and lateral expansion of the zygomatic arches.

In rodents, in relation to the anteroposterior (propalinal) movements of the lower jaw, the glenoid fossa is trough-like, elongated longitudinally and lacks the postglenoid process. Only in rodents and multituberculates among mammals the structure of the glenoid fossa allows the anteroposterior movements of the lower jaw. The glenoid fossae in multituberculates and rodents, however, are otherwise very different.

The backward sloping (anterodorsal to posteroventral) of the glenoid fossa in multituberculates is related to the structure of the condylar process (see below), which faces posteriorly or posterodorsally, rather than dorsally (as in therians). Because of such a position of the condylar process, and because of the slightly concave profile of the upper premolars and molars, only at the backward inclination of the glenoid fossa can lower and upper molars and posterior premolars come into occlusion during the power stroke. In rodents, in contrast, the glenoid fossa slopes forwards (anteroventral to posterodorsal). As the condylar process faces upwards, only an anterior inclination of the glenoid fossa allows the occlusion of the premolars and molars during the power stroke. Other characters of multituberculate glenoid fossa such as its large size, anterolateral (almost longitudinal) elongation, flat surface, and backward sloping are related to the structure of the condylar process of the dentary discussed below. We
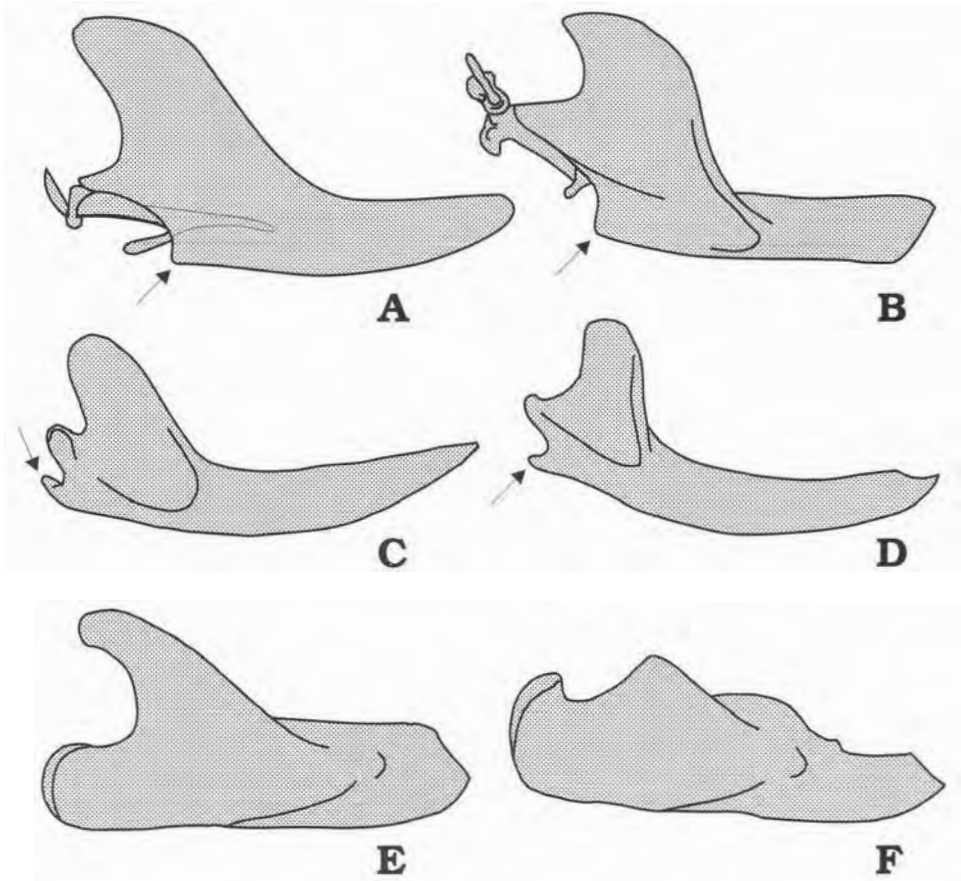
Fig. 14. Lower jaws in lateral view. ❑A. *Probainognathus*. ❑B. *Kayentatherium*. ❑C. *Didelphis*. ❑D. *Canis*. ❑E. *Kuehneodon*. ❑F. *Nemegtbaatar*. The arrows point to the angular process. Note the rounded posterior margin and structure of the condylar process in E and F. Not to scale. A, modified from Allin (1975); B, modified from Sues (1986); E, reconstructed after the photographs in Hahn (1978).

regard this suite of characters of the glenoid fossa, as a multituberculate autapomorphy.

Condylar process. — In mammals, except for the multituberculates and symmetrodonts, the posterior border of the dentary is primitively concave between the condylar and angular processes. In oldest triconodonts (*Morganucodon*) there is an angular process, which disappears in the Triconodontidae, Amphilestidae and Gobiconodontidae (Simpson 1928; Kermack *et al.* 1973; Lillegraven *et al.* 1979; Jenkins & Schaff 1988). In mammals with a double jaw joint, such as for example, *Morganucodon* and *Haldanodon* (Kermack *et al.* 1973; Lillegraven & Krusat 1991) and in embryos of extant mammals (e.g., Allin 1975; Maier 1989) this concavity houses the postdentary bones. In adult therian mammals (Fig. 14C, D) the concavity between the condylar and angular processes

(remnant of the accommodation of the postdentary bones) is present in all the Cretaceous therians, in insectivorous and carnivorous marsupials, in insectivores, bats, creodonts, carnivores, most condylarths, most rodents, primitive primates etc., but is secondarily lost in most herbivorous marsupials and placentals, in advanced primates, whales and in many other forms.

In multituberculates the posterior border of the dentary has a different structure (Fig. 14E, F). Hahn (1969, 1978) described the oldest known multituberculate lower jaws belonging to the plagiaulacoid Paulchoffatiidae. He noted that in this family the articular surface of the condyle faces posteriorly, and differs from that of later multituberculates in which it has a more dorsal orientation. Bakker & Carpenter (1990: Fig. 9) presented a composite drawing showing the upward shift of the condyle in the evolution of multituberculates. In most multituberculates (Figs 1, 3), except for specialized forms such as some Taeniolabididae and the Sloanbaataridae (Fig. 17B, C), the condylar process slopes posteriorly and contributes to the posterior margin of the lower jaw, not forming a well delimited process, as in Theria. In most Theria the condylar process is transversely elongated, but in rodents, in relation to the anteroposterior movements of the lower jaw the condylar process is narrow and is sometimes (e.g., in *Cricetus*) bent posteriorly as in multituberculates. In such cases in rodents the posterior border of the dentary is incurved below the process, as characteristic of non-specialized Theria. In multituberculates, in contrast, the condylar process is continuous with the remainder of the posterior border of the dentary which forms a semicircle (Figs 14E, F, 15A). We regard the semicircular, posterior border of the dentary with a condylar process forming at least a part of it, as an autapomorphy of multituberculates.

Jenkins *et al.* (1983) suggested that the angular process in non-mammalian synapsids and in non-therian mammals is not homologous to the angular process in therians and should be called 'pseudoangular process'. Sues (1986) challenged this idea and demonstrated the homology of this process in therians and tritylodontids (Fig. 14B in this paper). Reconstructions of the synapsid lower jaws in evolution leading to mammals by Allin (1975: Pl. 3; see also Fig. 14A of *Probainognathus* in this paper) also show this homology. Sues (1986: p. 254) stated: "It is apparent from examination of [...] *Dinnetherium* that the 'angular process' (in Jenkins *et al.* 1983 sense) is produced by downward growth of the lateral ridge of the articular process. 'Fusion' of this process with the 'pseudoangular process' could have produced the condition in the Multituberculata, Symmetrodonta, and Triconodonta (Simpson 1928: Figs 9, 19) where the ventral margin of the dentary is continuous from symphysis to condyle".

In multituberculates, the posterior portion of the ventral margin of the dentary has an internal shelf, called pterygoideus shelf, floor of the pterygoid fossa, inflected flange etc. Miao (1988) discussed the old, but subsequently abandoned idea of Falconer (1857) and Cope (1881), that the pterygoideus shelf represents the inflected angular process. This shelf,
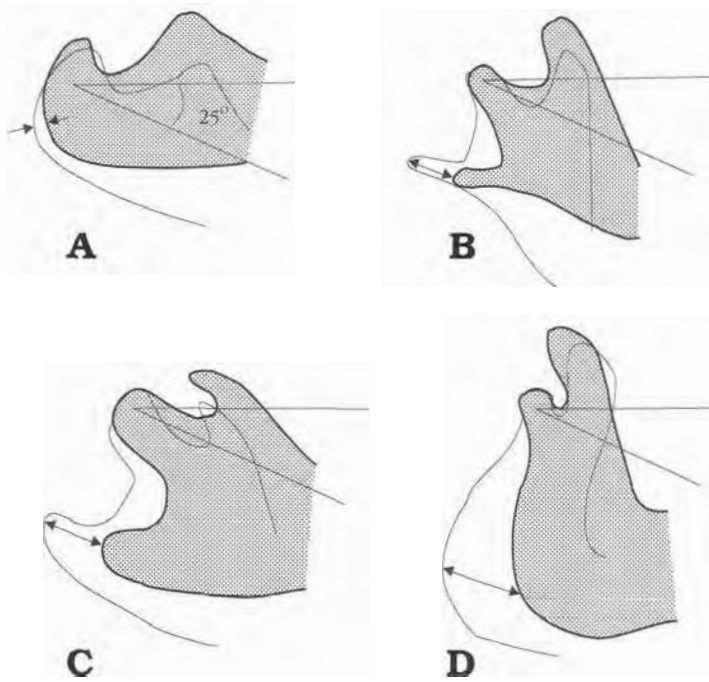
Fig. 15. Comparison of the movement of the posterior margin of the lower jaw during the opening of the mouth, with all the jaws rendered to the same length. □A. *Nemegtbaatar.* □B. *Paraechinus.* □C. *Rattus.* □D. *Equus.* In *Nemegtbaatar* the angular process disappeared. In *Equus* only the remnant of the angular process has been preserved and forms a prominent, rounded angle of the dentary; the concavity between it and the condylar process is very shallow. Bold lines and hatched areas — position of the jaw with mouth closed (horizontal line); normal lines — position with mouth open at 25°; arrows — distance between the initial and final position of the posterior margin.

however, incorporates not only the angular process (if it was present in earliest multituberculates), but the entire portion of the ventral margin of the lower jaw below the mandibular canal. Both this extensive pterygoideus shelf in multituberculates and the angular process in therians are sites for insertion of m. pterygoideus, and thus are homologous in the musculature that inserts upon them. Maier (1987) speculated that the inflected angular process in marsupials is related to sound transmission. The different portions of the dentaries that are inflected in multituberculates and in therians, strongly suggest that the inflection occurred separately. In marsupials the remnant of the housing of the postdentary bones is well seen above the posterior end of the inflected angular process (Figs 12A, C, E, 14C), while in multituberculates this remnant cannot be discerned even in the most completely preserved dentaries (Figs 4, 12G, H, 14E, F). The oldest known Late Jurassic multituberculate dentaries display the usual multituberculate structure (Fig. 14E; and Hahn 1969, 1978), with a strong degree of inflection and no trace of the remnant of the housing of the postdentary bones.

We speculate on why the angular process is absent in multituberculates. If in multituberculates the mouth opens, for example, 25° during the preparatory stroke, backward movement of the posterior margin of the lower jaw is only slight (Fig. 15A). In Theria the distance between the two positions of the posterior margin of the lower jaw, during the opening is 3–4 times greater (than in multituberculates) in insectivorous (Fig. 15B) and in carnivorous mammals (not figured), 5–6 times greater in small herbivores (Fig. 15C), and 6–8 times greater in large herbivores (Fig. 15D). In Theria the presence of an angular process (secondarily lost in e.g., large herbivores and primates, and forming a rounded angle of the dentary) causes an increase of the protractory horizontal component of the vector of masseter superficialis. Because of the backward (retractory) masticatory power stroke in multituberculates, the masseter superficialis inserted more anteriorly than in Theria, and masseter lateralis profundus (which had only a small horizontal protractory vector component; Tables 2, 3) inserted at the posteroventral part of the dentary. Had there been a large horizontal protractory vector component associated with an angular process in multituberculates, this would prevent a backward movement, and thus we conclude that the absence of an angular process is related to the backward (retractory) power stroke.

The unique structure of the multituberculate condylar process is related to the structure of the glenoid fossa. Wall & Krause (1992) provided a thorough analysis of the structure and working of the condylar process in *Ptilodus* (where it is situated below the occlusal surface of the molars), and discussed it in respect to the size of the coronoid process, and consequently the size of the temporal muscle. They reconstructed in *Ptilodus* a translation of the condylar process during the recovery stroke along the glenoid fossa, including rotation of the process about the transverse axis, resulting in a large gape. It follows from their study that the backward sloping of the condyle in multituberculates is related to the ability to gape the mouth.

In most multituberculates, including the Paulchoffatiidae (Hahn 1969, 1978; Clemens & Kielan-Jaworowska 1979), Plagiaulacidae (Simpson 1928, 1929; Ride 1957; Bakker & Carpenter 1990), all the Asian Eucosmodontidae (Kielan-Jaworowska 1970, 1971, 1974), possibly also all the North American Eucosmodontidae, including *Eucosmodon gratus* (Jepsen 1940), *Stygimys kuszmauli* (Sloan & Van Valen 1965), and the following Ptilodontoidea: *Mesodma ambigua, Mimetodon churchilli* (Jepsen 1940) and *Ptilodus montanus* (Krause 1982; Wall & Krause 1992), the articulating surface of the condyle is placed below, or at about the level of the occlusal surface of the molars, and forms an arch occupying the posterodorsal corner of the jaw. In *Nemegtbaatar* (Fig. 3) the upper part of the condyle is placed above the occlusal surface, the lower part of the condyle below this surface. With a low position of the condylar process, the angle between the occlusal level of the molars and the lower margin of the jaw varies between 8° in *Kuehneodon* (measured on the photographs of Hahn
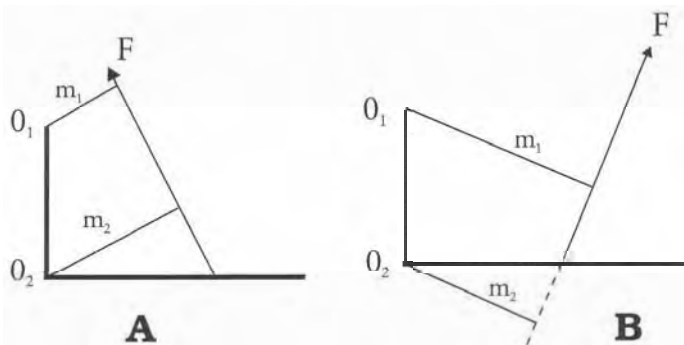
Fig. 16. Diagram illustrating the moment arm of the resultant forces of all the masticatory muscles, generated on the teeth during the power stroke. A. Lower jaw in multituberculates, with retractory horizontal component of the resultant force. B. Lower jaw in herbivorous therians (e.g., rodents) with protractory horizontal component of the resultant force. Bold lines: horizontal — lower jaw at the level of the molars, anterior is to the right; vertical — posterior margin of the lower jaw; F — vector of the resultant force of the masticatory muscles during the power stroke; m_1, m_2 — moment arm of F with the high and low positions of the condylar process; O_1 — condylar process situated above the level of the molars; O_2 — condylar process situated at the level of the molars.

1978), 11–12° in *Nemegtbaatar*, and 14–15° in *Chulsanbaatar*. In the Plagiaulacidae the fragmentary lower jaw with the condylar process has been preserved only in the plagiaulacine *Plagiaulax becklesii* (Simpson 1928: Pl. 3: 2), and in the allodontine *Ctenacodon serratus* (Simpson 1929: Pl. 1: 1). In these photographs and the correct drawings and reconstructions of Falconer (1857: Figs 11–14), Owen (1871: Pl. 4: 10–15), and Ride (1957: Fig. 1) the condylar process is situated at about the level of the occlusal surface of the molars. This contrasts with the reconstructions of Gidley (1909: Fig. 9) and Simpson (1926: Figs 5–7; 1928: Fig. 9; 1929: Figs 4–5), where the condylar process is placed above the level of the molars.

In the monotypic Sloanbaataridae represented by *Sloanbaatar* (Fig. 17C, and Kielan-Jaworowska 1970, 1971) and in the Taeniolabididae (Fig. 17B, and Kielan-Jaworowska 1974; Miao 1988), the condylar process has a different construction. The articulating surface is situated higher than the occlusal level of the molars, the jaw below the process is narrow in lateral view; the articulating surface does not extend so far on the posterior surface of the jaw as in the Plagiaulacoidea and in other forms with a low condyle; the angle between the lower margin of the jaw and the level of the occlusal surface of the molars is greater and varies between 26° in *Catopsbaatar* and 30° in *Sloanbaatar*. The entire lower jaws of the Taeniolabididae have been preserved only in *Catopsbaatar catopsaloides* (Kielan-Jaworowska 1974), *Lambdopsalis bulla* (Miao 1988) and (almost complete) in *Taeniolabis taoensis* (Broom 1914; Granger & Simpson 1929).

Several incomplete lower jaws belonging to the Plagiaulacoidea, Eucosmodontidae or Ptilodontoidea have been reconstructed with a highly placed condylar process, in addition to the above cited reconstructions of

Gidley and of Simpson, by Jepsen (1940), Sloan & Van Valen (1965) and Sloan (1979). As we have not seen the original materials, it is difficult to venture an opinion as to how reliable these reconstructions are.

The low position of the multituberculate condylar process characteristic of most multituberculates, may be explained in terms of functional anatomy. In extant herbivorous therian mammals the grinding action involves the strong vertical component of the resultant force of the masticatory muscles. In extant rodents the condylar process is always situated above the level of the molars. In fossorial rodents that dig with the incisors, the great vertical component of the force of masticatory muscles is necessary. In fourteen species of fossorial rodents, belonging to the Spalacidae, Myospalacidae, Cricetidae, Bathyergidae, Geomyidae and Rhizomyidae, the height of the distance between the condylar process and the level of the molars varies between 17–22% of the condylobasal length of the skull; in non-fossorial rodents belonging to 40 species of 8 families, this height varies from 9–13% (measured by G.E. Zubtsova in ZIN collection).

In Fig. 16 we present a diagram showing why with the backward direction of the resultant force, the low position of the condylar process (at about the level of the molars or below) should be advantageous. Had the condylar process (the temporomandibular joint) been placed in multituberculates (Fig. 16A) above the level of the molars, the moment arm of the resultant force of all the masticatory muscles (m_1) would be smaller than with the condylar process situated at the level of the molars (m_2). In therians (Fig. 16B) the moment arm (m_1) would be greater with the condylar process placed above the level of the molars, than with the condylar process situated at the level of the molars (m_2).

Speculations on multituberculate diet

Adaptations for cutting resistant items (Figs 17, 18). — We argued in the preceding section that in relation to the backward chewing, the low position of the condylar process should be advantageous for multituberculates. The question arises why then is this process situated high in respect to the occlusal surface of the molars, in the Taeniolabididae and Sloanbaataridae? In an attempt to answer this question we speculate on different strategies employed by these groups for cutting resistant items (Fig 17).

Wall & Krause (1992) demonstrated, that due to the structure of the condylar process, *Ptilodus* was unable to eat *Ginkgo* seeds of the diameter 12 mm, and concluded that the upper size limit of its food was of approximately 10 mm for relatively resistant items (see also Del Tredici 1989). The powerful taeniolabidoid incisors with limited enamel band, similar to those of rodents, were well adapted for cutting hard seeds. In the Eucosmodontidae and Sloanbaataridae the fourth premolars assisted the incisors in their cutting function, in the Taeniolabididae, the fourth
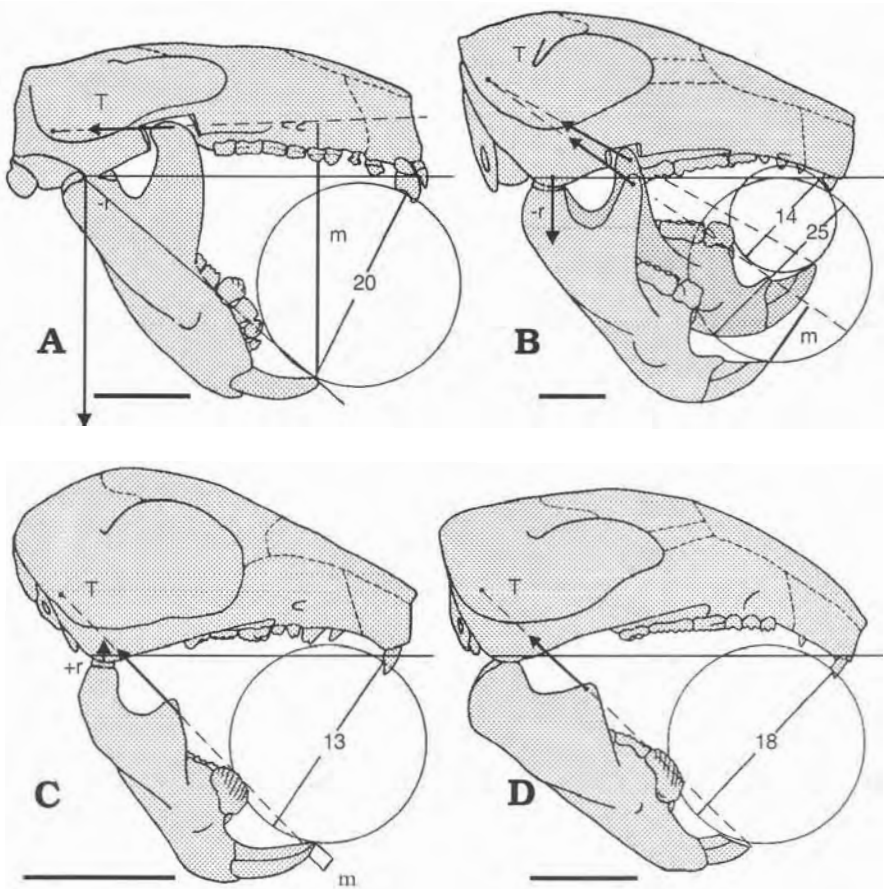
Fig. 17. Opening of the mouth during the slicing-crushing action. ⊐A. A hypothetical paulchoffatiid. ⊔B. *Catopsbaatar*. ⊔C. *Sloanbaatar*. ⊔D. *Nemegtbaatar*. A, modified from reconstructions of *Paulchoffatia* and *Pseudobolodon* by Hahn (1985 and 1994 respectively), with the postorbital process placed posteriorly and with a lower jaw of *Kuehneodon*. T — vector of temporalis pars posterior (arrow) and its extensions (broken lines); black points — centers of the attachments areas of temporalis p. posterior; large circles — size of seeds with diameters in mm; m — moment arms of the dislocation or pressing force generated at the incisor; -r, +r — dislocation and pressing forces generated at the condylar process respectively. The angle in A, between the horizontal line and the line extended from the fulcrum of the temporomandibular joint to the tip of the lower incisors, shows how the gape was measured in all the taxa. Scale bars — 10 mm.

premolars became gradually reduced and the incisors entirely overtook the cutting.

In Fig. 17 we compare the gape in a paulchoffatiid multituberculate (A), *Catopsbaatar* (B), *Sloanbaatar* (C) and *Nemegtbaatar* (D), and the forces generated at the temporomandibular joint due to the action of m. temporalis pars posterior (referred to further for the sake of brevity as m. temporalis).

In a paulchoffatiid multituberculate (Fig. 17A) at a gape of 40° (measured between the horizontal line and line from the fulcrum of the temporomandibular joint to the tip of the lower incisor), the anterior extension of the vector of m. temporalis passes high above the tip of the incisor and the force generated at the condylar process (using the bifurcal model of Bramble 1978) is directed downwards, causing a strong dislocation of the joint. Paulchoffatiids had the largest coronoid process among the multituberculates, which increased the moment arm of m. temporalis, needed for generating the strong biting force at the incisors. We agree with Clemens & Kielan-Jaworowska (1979) and Krause (1982) that most multituberculates were omnivorous. As argued on p. 95, the paulchoffatiids possibly used their big incisors for picking up and killing insects, but they also included other invertebrates and plants in their diet. As inferred from the strong dislocation force generated at the temporomandibular joint, they possibly were not adapted to slice large hard seeds, for which a large gape is needed (see below).

In *Catopsbaatar* at a gape of 40° (lower gape in Fig. 17B), the anterior extension of the vector of m. temporalis passes above the tip of the incisor and the force generated at the condylar process will be directed downwards and will cause dislocation of the joint. This force was, however, smaller than in paulchoffatiids. In *Catopsbaatar* the coronoid process is higher than in *Nemegtbaatar* and *Sloanbaatar*, but lower than in paulchoffatiids. *Catopsbaatar* is approximately 1.5 times larger than *Nemegtbaatar*, more than twice as large as *Sloanbaatar* and three times larger than *Chulsanbaatar*. Therefore in order to crush hard seeds of 12–14 mm diameter, it would be sufficient for it to open its mouth only 25°. At such a gape (upper gape in Fig. 17B), the extension of m. temporalis vector would reach the tip of the lower incisor and would not generate the dislocation force at the temporomandibular joint. If at a gape of 25° one would lower the condylar process to the position as, for instance, in *Nemegtbaatar*, because of the high coronoid process the dislocation force would appear. On the other hand a high coronoid process was needed to generate strong force at the incisors, which in all the Taeniolabididae acquired a gnawing function.

In *Sloanbaatar* (Fig. 17C), at a gape of 40°, the extension of m. temporalis passes below the tip of the incisor, and the force generated at the temporomandibular joint pushes the condylar process upwards, as should be expected for the efficient action of the joint. If in *Sloanbaatar* one would lower the high condylar process to the same position as in *Nemegtbaatar*, then the extension of the vector of m. temporalis would pass as high as in *Catopsbaatar*, which would cause dislocation of the temporomandibular joint. The coronoid process in *Sloanbaatar* is relatively low. If one would enlarge it to the height proportional to that of *Catopsbaatar*, this would also result in dislocation of the temporomandibular joint. These are the reasons for the high position of the condylar process and low coronoid process in *Sloanbaatar*.
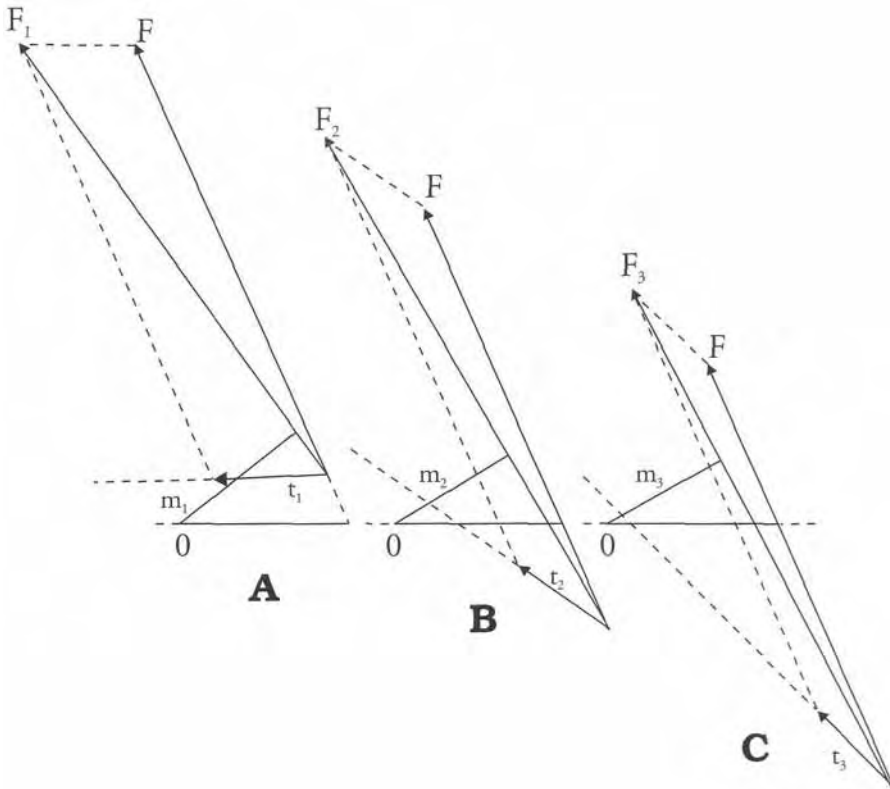
Fig. 18. Diagram showing the influence of the vector of temporalis pars posterior, on the resultant force of all the muscles. ❑A. A paulchoffatiid. ❑B. *Catopsbaatar.* ❑C. *Sloanbaatar.* F — resultant force of all the vectors without vector of temporalis p. posterior in all three taxa; F_1, F_2, F_3 — resultant force of all the vectors including temporalis posterior in three taxa; m_1, m_2, m_3 — moment arms of the forces F_1, F_2, F_3; 0 — rotation center at the condylar joint; t_1, t_2, t_3 — vectors of temporalis p. posterior for three taxa (as shown in Fig. 17).

In *Nemegtbaatar* (Fig. 17D), at a gape of 40° the extension of the vector passes along the tip of the incisor and is neutral to the temporomandibular joint. The coronoid process in *Nemegtbaatar* is very low; if one would enlarge this process, for instance, to the height of that in *Catopsbaatar*, then the force generated at the condylar process would be directed downwards and would cause dislocation.

We discussed above the action of a single muscle (m. temporalis), rather than the resultant force of all masticatory muscles. Study of the action of single muscles helps to understand the action of the resultant force. In Fig. 18 we present an attempt to analyze the resultant force of all the muscles without m. temporalis, adding to it the vector of m. temporalis (as shown in Fig. 17) in three different taxa, all at a gape of 40°: in a paulchoffatiid, where because of a large coronoid process, the dislocation force is the greatest; in *Catopsbaatar*, where dislocation force at the temporomandibular joint exists, but is smaller than in a paulchoffatiid; in

Sloanbaatar where the action of temporalis does not produce dislocation force at the temporomandibular joint and pushes the condylar process upwards.

As seen in Fig. 18, in a paulchoffatiid, with the greatest dislocation force, the resultant force of all the masticatory muscles is the smallest. In *Catopsbaatar* the dislocation force is smaller and the resultant force is 10% greater than in a paulchoffatiid. In *Sloanbaatar* in which there is no dislocation force, the resultant force is 19% greater than in a paulchoffatiid. This shows that the dislocation force diminishes the resultant force, and particular taxa developed the adaptations to avoid it, such a high condylar process and different sizes of the coronoid process.

We conclude that the adaptation for crushing large hard seeds, in extreme cases worked in multituberculates against the benefit of the low position of the condylar process.

The problem of *Chulsanbaatar*. — *Chulsanbaatar*, because of its small size was not able to eat seeds larger than 7–8 mm in diameter. It had to break the seeds with the incisors gradually, gnawing them as modern rodents do. The broken seeds were subsequently sliced and ground by the premolars and molars as in other multituberculates. With the growth of the animal the size of the anterior margin of the incisors increased roughly linearly, the cross-sectional area of the muscles increased with a square. Therefore small animals such as *Chulsanbaatar* needed special adaptations to increase the force generated on the incisors. Anterior migration of the insertion of the masticatory muscles, which increased the moment arm of these muscles, is such an adaptation. Masseter medialis pars anterior inserted in *Chulsanbaatar* in a very deep masseteric fovea (number 8 in Fig. 2C), and the distance between the anterior margin of it and the end of the jaw amounts to 76% of jaw length; in other multituberculates it amounts to 62–69%, in rodents (measured to the anterior margin of the insertion of the muscle) and in small herbivorous marsupials it is less than 55% (Fig. 12). As may be seen in Table 4, other masticatory muscles also inserted more anteriorly in *Chulsanbaatar* than in other multituberculates and in rodents, increasing the forces generated by these muscles.

At a muscle contraction greater than 30% of resting length, their force strongly diminishes (Gordon *at al.* 1966; Alexander 1989). The topography of muscles in mammals therefore, as a rule, corresponds to work within a frame of optimal contraction. A more anterior insertion of masseter medialis pars anterior and masseter superficialis pars anterior in multituberculates is limited by the optimal limit of contraction. Comparison of the open (measured at the maximal possible gape of 45°, which possibly was not used by all these taxa) and the closed mouth in *Chulsanbaatar* and in other studied multituberculates, shows that when the mouth closed in *Chulsanbaatar*, masseter medialis pars anterior, contracted 39%, in *Catopsbaatar* 37%, in *Nemegtbaatar* 40% and in *Sloanbaatar* 41%. The relatively small contraction of this muscle in spite

of its anterior insertion in *Chulsanbaatar*, may be explained by its elongation caused by its more ventral insertion than in other taxa (Fig. 2C). Masseter superficialis pars anterior is a relatively short muscle, and in all studied taxa it contracted 40%. Its more anterior insertion was not possible, as it would cause its further contraction, which would overcome the optimal action of the muscle, and would cause the dislocation at the temporomandibular joint.

Function of incisors. — Only some of extant therian mammals, with teeth adapted to eating plants, are exclusively herbivorous. Most of them (e.g., most rodents, numerous Artiodactyla, some marsupials etc.) (Frechkop 1955; Yegorov 1965; Landry 1970; Dimpel & Calaby 1972; Fokin 1978; Nowak & Paradiso 1983 and references therein) in addition to plant food eat also insects, worms, small mammals etc.

The so called 'plagiaulacoid' dentition, characteristic of multituberculates and defined by Simpson (1933: p. 97) as 'that in which one or more of the lower cheek teeth are modified into large, simple, laterally compressed blades with serrated cutting edges', developed in parallel in several groups of living and extinct mammals. It occurs in four living genera of diprotodontid marsupials, in extinct abderitine and polydolopid marsupials, and in carpolestid primates (Simpson 1926, 1933; Clemens & Kielan-Jaworowska 1979; Parker 1977; Krause 1982). Calaby (1971) and Dimpel & Calaby (1972) demonstrated that the macropodid *Hypsiprymnodon* and the burramyid *Burramys*, both with 'plagiaulacoid' premolars, pick up insects with the incisors, and use the premolars for cutting up insects with hard cuticles, plants and worms (see also Clemens & Kielan-Jaworowska 1979).

Bicuspid upper incisors occur in some plesiadapiform primates (Gingerich 1976; Szalay & Delson 1979; Krause 1984) and often in extant insectivores, e.g., in the Soricidae (Gromov *et al.* 1963; Churchfield 1990 and many others) and in some Tenrecidae and Chrysochloridae (Grassé 1955; Heim de Balsac & Bourlière 1955). The bicuspid upper incisors and pointed, procumbent lower ones form an efficient grasping mechanism used by shrews for picking up and killing insects (Churchfield 1990).

The Haramiyidae, regarded as the oldest multituberculates (Hahn 1973; Sigogneau-Russell 1989), but more recently as a sister group of multituberculates (Butler & MacIntyre 1994; see also Sigogneau-Russell & Hahn 1994), have bicuspid upper incisors, with the anterior cusp higher than the posterior, and procumbent lower incisors. Similar structure of the upper incisors (I2) is characteristic of all the Jurassic multituberculates (Paulchoffatiidae and Plagiaulacidae) and of an unidentified Early Cretaceous multituberculate from Mongolia (belonging to the Plagiaulacoidea or to a suborder *incertae sedis*); the lower incisors in Plagiaulacoidea are large and semi-procumbent (Hahn 1969, 1978, 1987; Simpson 1928, 1929; Clemens & Kielan-Jaworowska 1979; Kielan-Jaworowska *et al.* 1987; Bakker & Carpenter 1990; Kielan-Jaworowska & Ensom 1992).

In the Ptilodontoidea the upper incisors are mostly unicuspid (Jepsen 1940; Simpson 1937; Clemens & Kielan-Jaworowska 1979; Krause 1982). Thin upper incisors characteristic of almost all Ptilodontoidea, are similar to those in the extant marsupial *Caenolestes* (see e.g., Gambaryan 1989), which uses the pointed upper and lower incisors as a powerful weapon for picking up and killing insects (Nowak & Paradiso 1983). In the Cimolomyidae (suborder *incertae sedis*, Clemens 1963; Archibald 1982) the upper incisors in *Meniscoessus* are large and tricuspid, and the lower ones are large with a row of serrations along the upper edge. This group is poorly known and no attempt has been made to reconstruct its feeding habits. We speculate that the bicuspid or thin and pointed upper incisors and the semi-procumbent and pointed lower incisors played in multituberculates a role similar to that described above in modern mammals.

The upper incisors of the Taeniolabididae differ from those in most other multituberculates in being unicuspid, or having only a tiny posterior cuspule. The Eucosmodontidae were originally defined by Jepsen (1940) as having bicuspid upper incisors, but all Asian eucosmodontid taxa studied here, have unicuspid upper incisors. Sloan & Van Valen (1965) recognized the gnawing function of incisors with a limited enamel band in the Taeniolabidoidea. Incisors acquired the gnawing action in multituberculate evolution only in the Taeniolabidoidea (but see Engelmann *et al.* 1990, who reported the presence of a limited enamel band in Late Jurassic 'plagiaulacoid' multituberculates). While the Ptilodontoidea with thin incisors and high cutting lower premolars were omnivorous (Krause 1982), the specialized Taeniolabidoidea, especially the Taeniolabididae, that acquired strong gnawing incisors (Sloan & Van Valen 1965) and gradually lost cutting premolars, changed their diet to a more herbivorous one. This was reflected in a more powerful masticatory musculature in the Taeniolabididae than in other multituberculates.

Multituberculates differ from rodents not only in having backward chewing stroke, but also, as demonstrated by Krause (1982) in lack of the transverse component of jaw movement. This difference results in a different structure of the incisors in these groups. In rodents the longitudinal and transverse diameters of the incisors are of the same length, or the transverse diameter is larger (Zubtsova 1986); in multituberculates, because of the lack of the transverse component in the jaw movement, the transverse diameter of the incisors is small in respect to the longitudinal one.

Comparison with the Tritylodontidae

The Tritylodontidae resemble the Multituberculata in the external structure of the skull to such degree, that until the 1940s they were regarded as primitive mammals related to the multituberculates. Kemp (1982, 1983) regarded the tritylodontids as a sister group of mammals. The

superficial similarities in the skull structure of the tritylodontids and mammals concern the presence of a diastema; absence of canines; possession of multicuspid cheek-teeth; and a backward movement of the lower jaw during the power stroke (Kemp 1982, 1983; Sues 1986). There are well known differences between the two groups, resulting from the non-mammalian status of the Tritylodontidae, such as the reptilian structure of the lower jaw and jaw joint, a less expanded braincase in the Tritylodontidae etc. (Kühne 1956; Hopson 1964; Kemp 1983; Sues 1985a, 1986 and references therein), which we do not discuss here.

We discuss below only some differences in the external structure of the skull, which are related to the function of the masticatory muscles. The zygomatic arch is deeper, and the ascending ramus of the dentary (and the coronoid process) is much higher in the tritylodontids than in the multituberculates. The sagittal crest is well developed in the tritylodontids and very weak or absent in the multituberculates, except for some specialized Taeniolabididae. The jaw joint (condylar process in multituberculates) is placed well above the level of the lower tooth row in tritylodontids, while in multituberculates it is placed below this level in the Plagiaulacoidea and most Cimolodonta, and above the level only in some advanced forms such as the Sloanbaataridae and Taeniolabididae (see discussion on pp. 90–94).

DeMar & Barghusen (1973) constructed a mathematical model of the mechanical arrangement of the lower jaw and the external adductor muscle in evolution of the synapsid jaw. They stated that (DeMar & Barghusen 1973: p. 637) 'it is unlikely that a coronoid process was initially developed by selection of a higher moment arm. We believe instead that selection for a posteriorly directed line of muscle action was the primary cause for the initial development of this process, and that such selection occurred in conjunction with the predatory habits of the advanced sphenacodontids'. Using their model Sues (1986: p. 256) suggested that the increase of the height of the coronoid process in tritylodontids 'relative to the condition in *Thrinaxodon*, provided the posterior temporalis with a much increased moment arm about the jaw joint'.

The coronoid process in multituberculates is the highest (which is a plesiomorphic feature) in the Paulchoffatiidae. The coronoid process substantially decreased in size in most Cimolodonta, increasing in size again in the Sloanbaataridae and advanced Taeniolabididae (see discussion on pp. 92 and 93).

Among the tritylodontid genera (Hopson & Kitching 1972; Kemp 1982; Sues 1986; Luo & Sun 1994 and references therein) the best preserved skulls are those of *Kayentatherium*. Sues (1986: Fig. 21) provided the diagrammatic reconstruction of the action of the adductor jaw muscles in *Kayentatherium* and discussed their function. His analysis has been largely based on Crompton (1963) and Barghusen (1968) papers, who offered detailed reconstruction of masticatory musculature in advanced non-mammalian synapsids (but not in the Tritylodontidae).

Comparison of Sues' (1986) reconstruction with those presented by us for Asian taeniolabidoid multituberculates (Figs 6, 7, 10) reveals important differences. The vector of the superficial masseter in *Kayentatherium* is directed anterodorsally, extending between the angular process of the dentary and the most anterior part of the zygomatic arch. In multituberculates we reconstruct the superficial masseter as separable into two parts (Figs 6, 7). The vectors of the superficial masseter are in multituberculates (Fig. 10) directed differently than in tritylodontids, the one for the anterior part of the muscle is directed dorsally, with a very slight posterior deviation, the second for the part posterior is still more strongly deviated posteriorly.

The vector of deep masseter (masseter medialis in our terminology) in *Kayentatherium* is directed dorsally with a posterior deviation, extending from the middle of the masseteric fossa to the medial part of the huge zygomatic arch. In multituberculates we regard masseter medialis as separable into three parts. The vectors of pars anterior and pars intermedia (the latter consisting of two bellies) are directed similarly to that of the deep masseter in *Kayentatherium*, but the vector of pars posterior is directed more posteriorly than dorsally, from the posterior elevation on the dentary towards the posterior zygomatic ridge at the end of zygomatic arch. The important difference is that in our reconstruction pars anterior of masseter medialis originates within the orbital pocket and inserts on the dentary much more anteriorly than in tritylodontids, in the masseteric fovea in front of the masseteric crest. Summing up, in multituberculates the masseter muscle as a whole inserted more anteriorly on the dentary than in tritylodontids.

Sues (1986) reconstructed m. temporalis in *Kayentatherium* as separable into two parts: pars anterior and pars posterior. The vector of pars anterior extends dorsally with a slight posterior deviation from the medial aspect of the ascending ramus of the dentary towards the lateral wall of the braincase, reaching the sagittal crest. The vector of pars posterior extends from the hook-shaped posterior extremity of the huge coronoid process posteriorly (with a small ventral deviation) towards the expanded posterodorsal portion of the temporal fossa, reaching the lambdoidal crest. Because of a very small coronoid process in studied multituberculates (especially in *Nemegtbaatar*, Fig. 10) the vectors of three parts of m. temporalis (pars superficialis, anterior and posterior) are directed differently than in *Kayentatherium*. We reconstructed pars superficialis and pars anterior as inserting by a common tendon in front of the coronoid process, while pars posterior inserted on the medial and lateral sides of the coronoid process. All three parts are reconstructed as originating to the rear of the postorbital process from a large area of the parietal bone below the weak sagittal and in front of the prominent lambdoidal crests (see pp. 58–60 for details). As a result their vectors extend from the area in front and on the coronoid process and diverge from one another posterodorsally (Fig. 10). The important difference is that, as in the case

of m. masseter, m. temporalis inserted in multituberculates on the dentary more anteriorly than in *Kayentatherium.*

Sues (1986) reconstructed the vector of external pterygoideus at the posterior part of the dentary, extending anteriorly with a small ventral deviation. In our reconstruction of multituberculates, m. pterygoideus is separated into two parts: p. medialis and p. lateralis. The vector of pterygoideus lateralis is similarly placed as that in *Kayentatherium*, differing in having a slight dorsal, rather than ventral deviation. The vector of pterygoideus medialis is situated more anteriorly and directed dorsally.

In spite of the differences in the arrangement of vectors of particular muscles, the multituberculates share with the tritylodontids the retractory horizontal components of the resultant force of all the masticatory muscles. The above comparison shows that although the tritylodontids and multituberculates resemble each other superficially in the structure of the dentition, as well as in using backward power stroke and bilateral mastication, their masticatory musculature differs considerably. As concluded by Sues (1986) the posterior temporalis was in tritylodontids the principal retractor of the lower jaw, while in multituberculates the masseter played a more important role.

We argued on p. 90, see also Fig. 16, that the low position of the jaw joint was advantageous for most multituberculates in relation to the backward power stroke employed by them. In tritylodontids, in spite of the backward power stroke the jaw joint was placed very high above the level of the cheek teeth, as in herbivorous therian mammals. The interpretation of its function is beyond the scope of the present paper. The above cited differences show that tritylodontids and multituberculates 'solved' the problem of employing the backward chewing stroke differently, and the backward chewing apparently developed independently in these groups.

Backward chewing occurred also in the traversodontid cynodonts, in which the power stroke was directed posterodorsally, rather than entirely posteriorly (Crompton 1972). The traversodontids may be ancestral to the tritylodontids (Crompton 1972; Sues 1985b), but see also Kemp's (1988) and Hopson's (1991) reviews of alternative opinions. Because of the dramatic differences in the skull and dentition, we do not provide a comparison of multituberculates and traversodontids.

Concluding remarks

Rensberger (1986) studied the transition from insectivory to ungulate herbivory in therian mammals that began near the Cretaceous-Tertiary boundary. A similar transition started in multituberculate evolution at the end of Triassic, at least 130 million of years earlier. There is so far no evidence for an insectivorous ancestor of multituberculates that would allow one to perform similar studies.
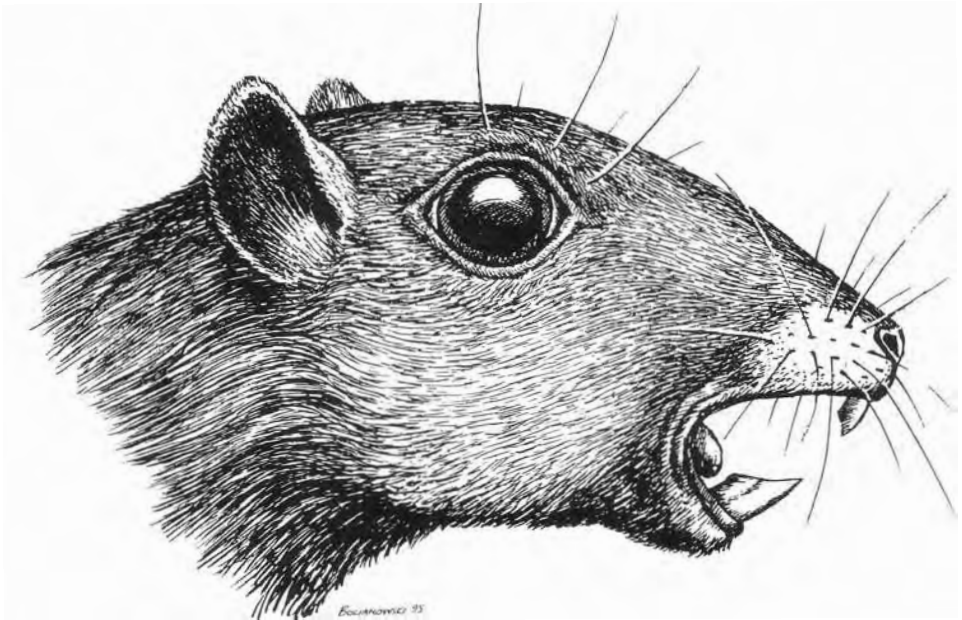
Fig. 19. Reconstruction of the head of *Nemegtbaatar*, approximately × 2.

The earliest triconodonts, which lay closer to the cynodont ancestors of mammals than any other group of early mammals, differ from advanced cynodonts, in that they possess unilateral occlusion that results in a triangular trajectory of the movement of the lower jaw (when viewed from in front) (Crompton 1974; Crompton & Hylander 1986). Primitive therians with tribosphenic molars, are also characterized by unilateral occlusion (Crompton & Hiiemae 1970; Crompton & Sita-Lumsden 1970). Bilateral occlusion was acquired secondarily among the therians, only in some rodents, and is correlated with the forward jaw movement during the power stroke (Turnbull 1970; Weijs 1994 and references therein).

During the course of this study we compared the multituberculate masticatory apparatus with that of rodents, to which it shows superficial similarity. Multituberculates share with rodents and with small herbivorous marsupials several characters acquired independently, and apparently were similar to rodents in the external appearance of the head (Fig. 19). It is beyond the scope of the present paper to review the immense literature on the diversified chewing mechanism in rodents (see Wood 1965; Hiiemae 1971; Weijs & Dantuma 1975; Weijs 1975, 1980, 1994 and Butler 1986, for framework and reviews). As summarized by Weijs (1994), in primitive rodents, although they acquired adaptations for gnawing with the incisors, jaw movements were virtually identical to those in primitive therian mammals, except that the power stroke was directed anteromedially rather than medially. From the primitive type of rodent mastication two

other patterns developed. For a superficial comparison with multituberculates, the most important is the type that occurs in myomorphs (rat and mole rat) and some hystricomorphs. Here occlusion is bilateral, the power stroke forward and a small transverse component of jaw movement is retained (Hiiemae & Ardran 1968; Hiiemae 1971; Weijs 1975; Weijs & Dantuma 1975). With backward chewing stroke it was virtually impossible to occlude the molars of one side without also occluding the molars on the opposite side, which suggests the bilateral mode of chewing in multituberculates, as earlier demonstrated by Wall & Krause (1992). We agree with these authors that multituberculates, similarly to modern rodents, could also use occasional unilateral mastication.

Hahn (1973) and Sigogneau-Russell (1989) regarded the Late Triassic and Early Jurassic Haramiyidae, known only from isolated teeth, as the earliest multituberculates. Butler & MacIntyre (1994) demonstrated that the Haramiyidae chewed backwards without any transverse component. They regarded the haramiyids as a sister-group of the multituberculates. Also Sigogneau-Russell & Hahn recently stated (1994, p. 209): 'We consider the enigmatic Haramiyidae to be related to the Multituberculata, and they may not be as closely related to the paulchoffattiids as we first thought (e.g., Hahn 1973)'. The oldest multituberculate Mojo is known only from a partial tooth (Hahn et al. 1989).

We argued elsewhere, on the basis of analysis of the postcranial anatomy that multituberculates may be a sister group of all other mammals (Kielan-Jaworowska & Gambaryan 1994). Conclusions from the present study are more equivocal. The multituberculate mode of chewing, with a backward power stroke (unique among mammals) and associated skull design, separate this group from all other mammals. However, given that in rodents the forward power stroke (with only a limited transverse component) developed from forms with a transversely directed power stroke, the origin of multituberculate backward power stroke from a transversely directed power stroke of triconodonts may be possible. As long as the cranial and postcranial anatomy of the earliest multituberculates remains unknown, it is impossible to determine whether multituberculates arose from a different cynodont stock than the triconodonts, and mammals are diphyletic, or whether the multituberculates arose from the triconodonts and mammals are monophyletic.

Acknowledgements

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